THE ADAPTIVE SIGNIFICANCE BY LAKEWARD MIGRATIONS BY JUVENILE ATLANTIC SALMON, SALMO SALAR L.

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THE ADAPTIVE SIGNIFICANCE OF LAKEWARD MIGRATIONS BY JUVENILE ATLANTIC SALMON, *Salmo salar* L.

BY

© Jeffrey Alexander Hutchings, B.Sc.

A thesis submitted to the School of Graduate Studies in partial fulfillment of the requirements for the degree of Master of Science

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ABSTRACT

Freshwater migratory patterns of juvenile Atlantic salmon, Salmo salar, were examined to (1) quantify parr movements into and out of lakes, (2) determine the importance of lakes to smolt production, and (3) identify mechanisms permitting the sympatry of anadromous and resident salmon. Counting fences were maintained at the mouth of Wings Brook, Newfoundland, and at the outlets of its two associated lakes. There was a lake- and seaward movement of parr from early-May to late-September, intensifying over a 6-8 week period during spring when smolt emigrated from the lakes. Lacustrine parr returned to the stream following either maturation (usually males) or smoltification (predominantly females). Lakes contributed 87-100% of the system's smolt production, provided conditions for increased parr growth and survival, and represented important overwintering habitat. Lakeward migrations appear to be innately controlled but regulated by the environment. My observations support the hypothesis that co-occurring anadromous and resident S. salar represent phenotypic polymorphism within a single population.

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Chapter 1

INTRODUCTION

Migrations in fishes are thought to be adaptive phenomena requisite to the enhancement of an individual's reproductive fitness through increased growth and survival (Heape 1931; Nikol'skii 1963; Harden Jones 1968; Northcote 1978, 1984). The heterogeneity of habitats in time and space allows organisms living in seasonally fluctuating environments to adopt those strategies that will maximize an individual's overall fitness.

The Salmonidae are an appropriate group in which to study migratory strategies because of the wide spectrum of migratory tendencies exhibited by its members (Hoar 1976). Two life history forms dominate the phenotypic milieu of many species within the Salmoninae (salmon, trout, char). The anadromous migrant form inhabits rivers and/or lakes during the juvenile stages prior to a seaward migration. These fish subsequently feed and usually mature at sea before returning to their natal streams to spawn.

Freshwater resident forms do not migrate to sea. This can be due to physical barriers within the stream that prevent either seaward movement or successful return to the spawning grounds. Anadromous and resident forms of sockeye salmon, Oncorhynchus nerka (Ricker 1940; McCart 1970), Atlantic salmon, Salmo salar (Berg 1948; Leggett and Power 1969), and Arctic char, Salvelinus alpinus (Nordeng 1983), frequently occur sympatrically.

Movements undertaken during juvenile stages will ultimately affect overall fitness if the habitats involved are sufficiently heterogeneous to impart differential growth and survival. This is an important consideration from both a management and an ecological perspective. Successful management and preservation of a species is contingent upon thorough knowledge of the habitats used by that species throughout its life. For migrating salmonids, it is necessary to identify the causal mechanisms responsible for initiating various movement patterns, and to assess the importance of these movements to a species' production. From an ecological perspective, varying patterns of migration can strongly influence life history strategies (Hutchings and Morris 1985). A study of movement patterns can lead to a comprehensive analysis as to how these strategies may arise and persist through time. Thus, the

nature of the selective pressures favouring anadromy and residency can be examined by evaluating the consequences of adopting different migratory strategies.

It is within these practical and conceptual frameworks that I have studied the freshwater movements of juvenile Atlantic salmon. My objectives are to (1) examine the movements of juvenile salmon into and out of lakes, (2) assess the importance of lacustrine habitat to Atlantic salmon production, and (3) identify mechanisms allowing for the sympatry of anadromous and resident forms.

The Atlantic salmon (Salmo salar Linnaeus 1758) occurs in both the anadromous migrant and freshwater resident forms throughout its geographical range (see Berg 1948; Scott and Crossman 1973; Ros 1981; Côté et al. 1984). The anadromous form matures at sea following a 1 to 8 year residence in fresh water, and returns to its natal stream to spawn. Freshwater resident salmon, or ouananiche (the Montagnais Indian name for this fish), complete their entire life cycle in fresh water.

The Atlantic salmon is indigenous to the basin of the North Atlantic Ocean (Berg 1948; Nielson 1961; Scott and Crossman 1973). Its Atlantic range extends from the Kapisigdlit River, Greenland, and numerous Icelandic rivers southward to the Douro River, Portugal, in the east and to

the Connecticut River, U.S.A., in the west. Its longitudinal range extends eastward to the Kara River, U.S.S.R., and westward to the Kogaluk River on the eastern shore of Hudson Bay, Canada. Until the late nineteenth century, the Atlantic salmon also occurred throughout the rivers of Lake Ontario (Fox 1930) and as far south as the Hudson River in eastern North America (Smith 1983).

The early experimental and descriptive work on the life history of Atlantic salmon was conducted in Europe, primarily Great Britain (inter alia Brown 1862; Paton 1898; Calderwood 1906; Hutton 1924), Germany (Miescher-Rusch 1883), Finland (Nordquist 1903, cited by Kendall 1935), and Norway (Dahl 1910). Atlantic salmon parr, the stage between absorption of the yolk sac and first migration to sea (Allan and Ritter 1977), were once erroneously thought to constitute a distinct species, Salmo salmulus (Scrope 1843). Shaw (1836) established the fallacy of this notion by rearing salmon ova and observing the developmental stages to maturity. He also found that the sperm of mature male parr, or "precocious" parr, could fertilize ova from adult anadromous females. Initial life history accounts of North American Salmo salar focussed on the ouananiche of New England (Atkins 1884) and Quebec (Chambers 1896). The first comprehensive description of the habits of anadromous salmon

in Canadian waters (Huntsman 1931) was preceded by a short series of communications from Quebec (Menzies 1925; Calderwood 1927), Newfoundland (Menzies 1929), Nova Scotia (Gilpin 1866), and New Brunswick (Perley 1850, cited by Kendall 1935) that dealt primarily with empirical and anecdotal accounts regarding the spawning migration of adult salmon.

Huntsman's (1931) brief treatment of juvenile Atlantic salmon is testament to the paucity of observational data relevent to this life history stage in the first part of the twentieth century. Kendall's (1935) discussion of parr was limited to length/age data at smoltification (the physiolological process undertaken by parr immediately prior to their first seaward migration) for a few New England rivers. He noted that "of this stage [parr] in our rivers very little has been observed" (Kendall 1935:55), a statement that arguably reflects our present knowledge of juvenile freshwater movements.

Kalleberg (1958) and Keenleyside and Yamamoto (1962) established the fact that parr maintain territories over stream substrate in riffles[1] primarily for feeding on

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1. Riffles are shallow (5-25 cm) stream sections of moderate current (>40 cm s^{-1}).

invertebrates drifting in the water column. Once these territories have been established in the spring, there is a strong tendancy for parr to remain in their territories throughout the growing season (Saunders and Gee 1964; Bulleid 1973). There is evidence to suggest, however, that instream movement does occur between riffle and pool habitats due to either fluctuating water levels (Saunders and Gee 1964) or changes in body size (Symons and Heland 1978).

Present knowledge of the freshwater movements/migrations by Atlantic salmon parr is based upon research that is largely descriptive in nature with little emphasis on the identification of causal mechanisms. This can be attributed to the fact that few studies have been initiated with the purpose of examining juvenile movements (notable exceptions are the studies of Saunders 1960, Saunders and Gee 1964, Buck and Youngson 1982, and Youngson et al. 1983).

The foregoing constraints notwithstanding, some generalizations can be made regarding the movements of juvenile Atlantic salmon in fresh water. Parr can undertake regular, directed downstream movements prior to smoltification. Autumnal emigrations of sexually immature parr from spawning tributaries and coastal rivers are often

undertaken by individuals that will smoltify the following spring (Calderwood 1906; Saunders 1960, 1976; Meister 1962; Fyefinch and Mills 1963; Elson et al. 1972; Youngson et al. 1983). Precociously mature male parr are known to participate in autumnal emigrations from tributaries of the rivers Dee (Buck and Youngson 1982) and Bran (Mills 1964) in Scotland, the Miramichi River in Canada (Saunders 1976), and the White Sea basin in the U.S.S.R. (Mel'nikova 1970). Dalley (1979) and Dalley et al. (1983) provided strong evidence for downstream and upstream autumnal migrations of precocious males to spawning grounds in Newfoundland. Downstream spring movements of parr coincide with the smolt migration in many Newfoundland rivers (Chadwick 1982a; Gibson 1983) but the significance and impetus for such movements are unknown.

Downstream parr movements recurring with varying or unknown regularity are known to occur from inlet streams into lakes (Huntsman 1945; Pepper 1976) and from rivers into estuaries (Huntsman 1945; Saunders 1960; Power and Shooner 1966; Chadwick 1982a). These movements are thought to be mediated by physical displacement through flood activity (Huntsman 1945; Power and Shooner 1966), high parr densities, low water levels, and high water temperatures (Chapman 1962; Pepper 1976; Gibson 1978a; Symons and Heland

1978).

Atlantic salmon parr of anadromous parents occur naturally in ponds and lakes throughout Newfoundland (Pepper 1976; Chadwick 1982b), and in southwestern Nova Scotia (R. L. Saunders, personal communication), however, exceedingly little is known about lakeward movements by juvenile salmon. Pepper (1976) reported a movement of one- to four-year-old parr from two inlet streams into a lake in central Newfoundland. Stuart (1957) noted that salmon parr accompany juvenile brown trout, Salmo trutta, in a spring upstream migration from a man-made reservoir into an inlet stream, returning to the reservoir in autumn. Lakeward movements from outlet streams warrant special consideration because of the active, directed nature of the migration, i.e. they cannot be simply displaced into the lake by spates. There are no published accounts of such movement by juvenile Atlantic salmon although periodic trapping of smolt at lake outlets indicates that such movement does occur (Pepper 1976; Chadwick 1982a).

Predicting the potential size of parr populations (an important component in assessing production) is customarily done by quantifying suitable stream habitat (Elson 1975). Utilization of lakes by juvenile salmon reduces the predictive power of stream-oriented models. The importance

of lacustrine habitat to the life cycle of anadromous Atlantic salmon, however, is not known. This is the premise under which I conducted my research.

Chapter 2

STUDY AREA

2.1 Wings Brook

Wings Brook and its associated lakes - Wings Pond and Bluehill Pond - are located within Terra Nova National Park (T.N.N.P.) in northeastern Newfoundland (Fig. 1). The park lies entirely on Precambrian rock (Baird 1966) and was completely ice-covered during the late-Wisconsin glaciation (Rogerson 1981). Climatic conditions are largely mediated by the cold Labrador current. The winters are moderately cold and the summers warm (e.g. mean maximum 1983 January and July air temperatures were -1.0° C and 22.9° C respectively). The lakes are generally ice-free from mid-April until late-December. Total precipitation for 1983 was 4.4 m, 20% of which fell as rain.

The outlets of Wings Pond and Bluehill Pond have been named Upper Wings Brook and Bluehill Brook. These second

order (Horton 1932) streams converge to form the main stem of Wings Brook 1.03 km from its mouth. The brook flows into a small (0.8 ha), shallow (z_{mean}=0.60 m), soft-bottomed basin, Wings Brook Cove, before emptying into a deep (z_{max}>34.0 m) and expansive (length=6.0 km, $width_{max}$=0.5 km) estuary, the southwestern arm of Alexander Bay (Bonavista Bay). Salinity data indicate that fresh water extends only slightly past the brook's mouth where it penetrates to a depth of about 50 cm (subject to tidal conditions). The halocline gradually deepens upriver into Wings Brook Cove which is fresh in the absence of strong southwest winds. A mid-summer halocline and thermocline exist in Southwest Arm at depths of 4-5 m (salinity range: 17.5-19.0 ppt surface to 27.0-29.0 ppt bottom [16.0 m]; temperature range: 17.0-18.0°C surface to 4.0-4.5°C bottom). Southwest Arm becomes Alexander Bay proper 12.3 km east of Wings Brook.

Water temperatures throughout Wings Brook and its tributaries ranged over 0-25°C from May 21-November 22, 1982, and over 6.0-27.5°C from May 5-September 29, 1983. Daily water temperature maxima were generally 5-7°C higher than their corresponding minima although differences in excess of 10°C did occur. Minimum and maximum stream

discharge rates during the 1982 field season were 0.14-1.10 $m^3 s^{-1}$, 0.07-0.81 $m^3 s^{-1}$, and 0.05-0.70 $m^3 s^{-1}$ for Wings Brook, Upper Wings Brook, and Bluehill Brook respectively.

Wings Brook, its tributaries, Wings Pond, and Bluehill Pond are collectively referred to as the Wings Brook system.

The fluvial environment of the Wings Brook system is small (Table 1) in comparison with most rivers supporting Atlantic salmon (see Porter et al. 1974). Stream water depths rarely exceed 60 cm. Short stretches of rapids exist in parts of the river but vertical heights in excess of 40 cm are absent. Shallow, riffle (83%) and run (12%) sections are abundant whereas deeper pool habitat is scarce (water type terminology follows Rimmer et al. [1983]). Bottom substrate is predominantly cobble/pebble (16-256 mm diameter) although a 20 m section of Bluehill Brook is comprised wholly of sand (0.06-2.00 mm diameter). Anion/cation concentrations, pH, alkalinity, hardness, turbidity, and specific conductivity are well within the normal range of values associated with rivers throughout insular Newfoundland (Murray and Harmon 1969; Department of Fisheries and Oceans, St. John's, unpublished data). Riparian vegetation provides considerable shade throughout the river's length. Plants providing cover include the

speckled alder, Alnus rugosa, black spruce, Picea mariana, mountain maple, Acer spicatum, and a variety of grasses and shrubs. Extremely large (80-100 mm length) freshwater clams, Margaritifera margaritifera, are abundant in the upper reaches of Upper Wings Brook.

2.2 Bluehill Pond

Bluehill Pond is a large (128 ha) lake with two distinct basins connected by a long, shallow channel. The north basin, Bluehill North, is much smaller (16.4 ha; z_{mean}=2.65 m; z_{max}=10.5 m) than the south basin, Bluehill South (111.4 ha; z_{mean}=9.23 m; z_{max}=22.6 m). Bluehill North lacks sufficient depth to permit formation of a hypolimnion whereas a thermocline is present in Bluehill South at depths of 9-11 m. Kerekes (1974) described the limnological conditions of Bluehill Pond based on data collected in 1969 and 1970. Surface water temperatures did not exceed 18.0°C in 1969 and 1982 in either basin. A comparison of the 1969-70 Bluehill North and 1982-83 Bluehill outlet data revealed little change in the chemical parameters measured in both studies (i.e. Ca^{2+}, SO_4^{2-}, Cl^-, specific

conductivity, pH, total alkalinity) over the 12-14 yr period. The exceptions were sulphate and hydrogen ion concentrations. The former decreased from 4.2 mg l^{-1} in 1969 to 1.6 mg l^{-1} in 1982. The surface waters of Bluehill Pond increased in acidity as the pH decreased from an average of 6.91±0.10 (n=9) in 1969 to 6.45±0.20 (n=11) and 6.37±0.13 (n=3) in 1982 and 1983 respectively. Small intermittant streams empty into the lake. The shoreline is mostly bedrock with a few sand beaches. Rooted aquatic vegetation (predominantly Nuphar variegatum) grows in the littoral zone of Bluehill North. Bluehill Pond supports fish populations of anadromous salmon and ouananiche, anadromous and non-anadromous brook char, Salvelinus fontinalis, non-anadromous Arctic char, S. alpinus, anadromous rainbow smelt, Osmerus mordax, and American eel, Anguilla rostrata.

A log jam, consisting of very large trees that had been cut at least 25 years ago, was located at the mouth of Bluehill Pond. Data collected in 1982 suggested that these logs were preventing fish passage from lake to outlet at low water levels. To test this hypothesis, the log jam was removed on May 19, 1983.

2.3 Wings Pond

Wings Pond (121.2 ha; z_{mean}=7.2 m; z_{max}=19.5 m) is similar in size to Bluehill Pond but its morphometry is quite different. Wings Pond is a single-basin, rectangular lake with a bottom that deepens gradually around its periphery. The waters of Little Wings Pond to the south and Jay Pond to the north drain into Wings Pond before flowing down Upper Wings Brook at the northwest corner of the lake. Despite its depth, Wings Pond does not thermally stratify. The lake is open to frequent, strong onshore (ocean) winds, and the resultant wind-induced mixing probably precludes formation of a thermocline. Water temperatures in July, 1982, did not exceed 20.0°C at the surface and 14.0°C at the bottom. The boulder-strewn shoreline is interrupted by two sandy beaches on the southwestern and southeastern shores. Water chemistry data recorded at the mouth of the lake in 1982 and 1983 indicate that the chemistry of Wings Pond is similar to that of Bluehill Pond (Table 2). The chemical parameter values (Table 2) measured at both lake outlets are in close agreement with those reported from five water basins in Terra Nova National Park (Kerekes 1974). Extensive bog occurs along the western shore with black spruce

dominating the remaining shoreline. Nuphar variegatum is present near the outlet and along much of the western half of the north shore. Wings Pond supports populations of anadromous salmon and ouananiche, anadromous and non-anadromous brook char, anadromous rainbow smelt, American eel, three-spine stickleback, Gasterosteus aculeatus, and four-spine stickleback, Apeltes quadracus.

Chapter 3

MATERIALS AND METHODS

3.1 Counting Fence Collections

Two-way fish counting fences (Anderson and McDonald 1978) were installed at the mouth of Wings Brook and at the lake outlets (Fig. 1). The traps permitted enumeration of all fish moving upstream and downstream at each site. Traps were normally checked 1 to 3 times daily on a continual basis from May through November, 1982, and May to October, 1983, (see Table 3 for dates of trap installation and removal). The lower trap (located at the mouth of the brook) was inoperative from October 2-4, 1982, due to heavy rains and high water levels.

Trap efficiency is dependent upon the nature of the fence material that extends from the trap entrances to the river banks. Galvanized fencing (6 mm^2 square mesh) was installed at the lake traps and used in conjunction with

steel conduit at the lower trap. The conduit were normally lined with black polyethylene except during periods of very high stream discharge. All traps were 100% efficient in capturing fish greater than 8 mm in thickness although the lower trap captured all fish when polyethelane was used. (An 8 mm body depth corresponds roughly to a salmonine fork length of 40 mm; Scott and Crossman 1973.)

Salmon parr and brook char were counted, measured (to the nearest 1 mm), and weighed (to the nearest 0.1 g) under anaesthetic. Two tablets of Alka-Seltzer (acetylsalicylic acid 648 mg, sodium bicarbonate 3800 mg, citric acid 2000 mg) dissolved in 6-8 litres of water anaesthetized fish by CO_2 saturation in about two minutes. Subsequent recovery was rapid and no deleterious effects were discernible. All fish were released in their original direction of travel following recovery. All other fish species were enumerated, and were measured to the nearest 1 mm.

Scale samples were removed from the left side between the base of the dorsal fin and the lateral line, mounted on acetate slides in the field, and stored in labelled envelopes. Scales were aged under 40X magnification using a Bausch and Lomb microprojector, following criteria established by Havey (1959). Lengths at earlier ages were calculated using Lee's (1920) formula:

$$Ln = a + (Lc - a)\ Sn/Sc$$

where Ln is the length of fish at age n, Lc is the length of fish at capture, Sn is the scale radius at age n, Sc is the scale radius at capture, and a is the intercept of the body length - scale radius regression[2]. Scale radius is the distance from the focus to the scale edge along the longest oral radius (Bagenal and Tesch 1978). The use of Lee's formula is preferable to the so-called "regression" methods that calculate length from the body-scale relationship alone because it corrects for differential scale size on a given fish and for the fact that not all fish of the same length in a population have scales of equal sizes (Carlander 1981). Lee's formula assumes that body growth is directly proportional to scale growth, an assumption which Hile's (1970) study supports. This method is also the most commonly employed, thus making it useful for comparative purposes. Age determinations were initially done by one person. (The 1982 and 1983 samples were read by different

---

2. Age as used here is not the true demographic age of the fish but is designated by reference to the annual marks - annuli - on the scales such that the time between successive periods of rapid growth equals one year.

individuals.) Several hundred samples from each year were re-read by qualified personnel of the Northwest Atlantic Fisheries Centre, St. John's, Newfoundland.

All salmon parr and brook char moving at the lake outlets were marked with partial fin clips to determine the period of residency in the lakes and river following initial movement into these environments. Fin clips used were as follows:

upstream at Wings Pd - adipose, upper caudal
upstream at Bluehill Pd - lower caudal
downstream at Wings Pd - left pelvic, adipose
downstream at Bluehill Pd - right pelvic, upper caudal

During the spawning run period (arbitrarily defined as October 5 to November 23 on the basis of movement patterns and sexual condition of fish) the following fin clips were used:

upstream at both lakes - adipose
downstream at Wings Pd - left pelvic
downstream at Bluehill Pd - right pelvic

Salmon smolt[3] were counted but not physically handled during the 1982 field season. In 1983, smolt emigrating from the lakes were marked with either a left (Wings Pond)

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3. Fully silvered salmon on their first seaward migration.

or right (Bluehill Pond) half pelvic fin clip. This was done to determine the proportion of smolt migrating to sea that originated in the lakes. Smolt were measured, weighed and aged following the procedures outlined for parr. Gonads were removed from a sample of 118 smolt and examined macroscopically.

3.2 Physical and Chemical Parameters

3.2.1 Physical Data

Maximum/minimum thermometers located at each of the three trap sites provided a daily record of water temperatures. Stream water levels were monitored at each site using metre sticks either attached to the traps or embedded in the stream substrate. Daily air temperatures and precipitation were measured at Terra Nova National Park's meteorological station located about 8 km from the study area.

The discharges of Wings Brook and its tributaries were determined throughout the study period, usually at very high and low water levels, to determine maximum and minimum flow rates. Measurements were made at each of the lake outlets

at their confluence and immediately above the lower trap at the mouth of Wings Brook. Discharge is a function of the water velocity and the cross-sectional area of the stream and was calculated using the equation (Davis 1938)

$$D = wdal/t,$$

where D = discharge, w = stream width, d = mean stream depth, a = friction coefficient, and l = the distance over which a floating object travels in time t. The friction coefficent equals 0.8 if the stream bed is rough and 0.9 if it is smooth e.g. mud, bedrock (Hynes 1970). A value of 0.8 was used for Wings Brook and its tributaries.

Surface current velocity was measured by timing the downstream passage of a rubber ball over a distance of four metres (five replicates). Cross-sectional areas were determined along three transects located at the extreme upstream and downstream points and at the mid-point of the 4 m section. Mean depth was calculated from the following equation using measurements (n) taken at 1/4 (d_1), 1/2 (d_2), and 3/4 (d_3) of the stream width:

$$d = (d_1 + d_2 + d_3)/(n + 1)$$

Discharges at each of the three transverse sections were averaged to determine a discharge value for a particular station.

Kerekes (1974) used an electronic depth recorder to compile bathymetric data on Bluehill Pond. The morphometry of Wings Pond, however, was unknown. Attempts to duplicate Kerekes' procedure were thwarted by equipment malfunctions, lake remoteness, and uncooperative weather/water conditions. Consequently the work was done during the winter. A series of diagonal transects (n=14) and corresponding compass headings were established a priori and plotted onto a map drawn from an aerial photograph of Wings Pond. An ice auger was used to cut holes (n=150) at 60 m intervals along each transect with the exception of openings made 3 m and 10 m from shore. Depths were recorded at each auger site using a calibrated lead line. Surface area was calculated using a planimeter and lake volume was determined by planimetric integration (Lind 1979). Mean depth equals volume X $(\text{area})^{-1}$.

3.2.2 Water Chemistry

Water samples were collected for chemical analysis throughout the 1982 field season from both riverine and

lacustrine waters. Samples were refrigerated 1 to 14 days prior to analysis, which was done at the Water Analysis Facility of Memorial University.

Stream samples were collected on a weekly basis from June 8 to September 28 immediately above each trap. Concentrations of calcium, nitrate, total phosphorus, sulphate, and chloride were determined in addition to total hardness, specific conductivity, turbidity, total alkalinity and pH. Limited stream sampling conducted in 1983 provided data on nitrate, total phosphorus, calcium, sulphate, and hydrogen ion concentrations.

Surface water samples from Wings Pond and the north and south basins of Bluehill Pond were analysed for total dissolved solids (TDS) concentrations. These samples were collected on a weekly basis from July 28 to September 14, 1982, from a canoe (Wings Pond) and by swimming (Bluehill Pond basins) over the deepest waters of each basin. Water temperatures were recorded during each sampling.

Temperature/salinity versus depth profiles were determined along a 500 m transect between Malady Head (opposite the mouth of Wings Brook) and the entrance to Wings Brook Cove. Measurements were recorded from a YSI conductivity meter and repeated on 18 occasions along the transect between July 19 and August 3, 1982, at both high

and low tides.

3.3 Statistical Analyses

3.3.1 Influence of Environmental Parameters on Movement

Relationships between environmental attributes and daily movements of parr into the lakes and estuary were examined using the stepwise multiple regression analysis of SPSSX (SPSS Inc. 1983). Environmental parameters included maximum and minimum daily water temperatures (MAXTEMP, MINTEMP), daily average water level (DEPTH), daily amount of precipitation (PRECIP), and the difference between daily maximum and minimum water temperatures (TEMPDIF), an approximation of the daily rate of temperature increase. The tolerance criteria used to specify variable inclusion into the equations were as follows: tolerance value of 0.01; probability of F to enter (PIN) value of 0.50; probability of F to remove (POUT) value of 0.55. To minimize bias in the analyses, the time periods were restricted to the peak months of movement into the lakes (May, June, July) and into the estuary (May, June). Explained variance was estimated as the square of the coefficient of multiple correlation (r^2)

adjusted for the number of independent variables in the equation and the number of cases involved (Nie et al. 1975:358).

3.3.2 Growth

Simple linear regressions of total scale radius with age were determined for both parr and smolt. Parr were classified into three categories:

1. lacustrine parr (emigrating from the lakes into the stream),
2. riverine parr (emigrating from the stream into the estuary),
3. estuarine parr (emigrating from the estuary into the stream).

Before examining differences in parr growth between habitats, it was necessary to validate the assumption that the rate at which scale radius increased with body length was equal among individuals. This assumption was found to be invalid among lacustrine, riverine, and estuarine parr, possibly due to seasonal changes in the body length-scale radius ratio (the majority of riverine parr were collected in the spring, estuarine parr throughout the summer, and

lacustrine parr in the autumn). Scale radii were thus transformed to ensure that a scale radius for a fish in one habitat corresponded to the same body length as an equivalent scale radius for a fish in an alternate habitat. Data for parr were standardized to remove seasonal effects using the following equation:

$$S_j = (m_j S_j + (b_j - b_i))/m_i ,$$

where S_j = transformed scale radius for fish of habitat j, S_j = original scale radius for fish of habitat j, m_i = slope of body length-scale radius regression for fish of habitat i, m_j = slope of body length-scale radius regression for fish of habitat j, b_i = y-intercept of body length-scale radius regression for fish of habitat i, and b_j = y-intercept of body length-scale radius regression for fish of habitat j.

Stepwise multiple regressions incorporating dummy variables, using the SPSSX Regression procedure (SPSS Inc. 1983), were employed to test for slope/intercept homogeneity among the linear relationships of scale radius with age. Growth during the first year of life was excluded in the between-habitat comparisons because all individuals remained

in the river during this time. Growth rates of smolt from Wings and Bluehill Ponds were compared in a similar fashion.

Differences in the mean scale radius attained by migrant (emigrating from the stream into the lakes), riverine (emigrating from the stream into the estuary), and mature lacustrine parr at the end of their first winter were examined using an analysis of variance (Sokal and Rohlf 1981). Data were $\log_{10}$-transformed to validate the assumption of variance homogeneity among samples.

The power function $W = aL^b$, where W=weight, L=length, and a and b are constants, served as an appropriate model for weight as a function of length (Ricker 1975). The parameters a and b were determined by logarithmically transforming the above equation into the form $\log_{10}W = \log_{10}a + b(\log_{10}L)$. Simple linear regressions of $\log_{10}$weight (g) with $\log_{10}$length (mm) were calculated by year, for each sample site, for all parr moving in a given direction (upstream or downstream).

3.4 Lake and Stream Collections of Parr

Collections of Salmo salar were made from Wings Pond in 1983. Lake resident parr were collected using a 10 m (1.9 cm stretch mesh) and a 38.5 m (5.1-6.7 cm stretch mesh) gill net set along most of the lake periphery. Both nets were fished on five occasions (22.0-24.5 hr per set) between September 21-29. The fish were measured, and then stored on crushed ice in a portable cooler immediately after capture. Scale samples were removed for age determination (see page 18) and sex was determined by macroscopic gonadal examination.

Stream collections of parr were made on six occasions between May 29 and August 17, 1982, and during August 17-23, 1983, from four sections of Wings Brook. Two sections were located 100-200 m above the lower counting fence over substrate comprised largely (85%) of cobble/pebble/rubble (lower section) and boulder/bedrock/rubble (see Hynes 1970 for terminology). Sections were also sampled midway between the junction of the tributaries and each of the lakes. Substrate ranged from pebbles to boulders at the Bluehill Brook site and the Upper Wings Brook section was comprised primarily (80%) of cobble, pebble, and rubble. Each section was subdivided into three electrofishing stations varying 30-50 m in length. Stations were blocked at their upstream and downstream ends by barrier nets (7 mm square mesh).

Parr were collected with a Smith-Root back pack electrofisher type VIII-A. Each station was completely electrofished a minimum of four times through a series of "sweeps" from the downstream barrier upstream to the upper net along transects across the river. Chi-square tests for goodness of fit (Sokal and Rohlf 1981) were performed to determine the degree to which the parr length-frequency distribution of a given section corresponded with the length-frequency distribution of parr emigrating from the stream terminus nearest to the electrofishing stations. Population estimates were calculated using the removal method (Zippin 1958). Biomass and population estimates were calculated from 1982 collections in the same stream sections.

Samples of ten parr from Wings Pond and lower Wings Brook were sent to Dr. Ulf Gyllensten, Department of Biochemistry, University of California, Berkeley, California, USA, for sequencing of mitochondrial DNA.

3.5 Removal of Bluehill Pond Log Jam

Data collected during the spring of 1982 suggested that a log jam located at the mouth of Bluehill Pond, about 50 m

above the counting fence, may have been preventing salmon smolt from leaving the lake at low water levels. During these periods of low discharge, the logs were often less than 10 cm above the stream bed. Following the removal of several logs on May 19, 1983, a channel approximately 3 m wide and 5 m long was formed.

3.6 Stream and Lake Surveys

The inlet streams of Wings and Bluehill Ponds were examined throughout the study period for possible use by salmon parr and ouananiche. Shallow sections along the periphery of Wings Pond were inspected in October and November, 1982, to determine whether the area was being used as spawning grounds. Wings Brook and its tributaries were repeatedly surveyed for a variety of reasons, including observations of spawning activities, mapping of stream substrate, and descriptions of surrounding flora.

Chapter 4

RESULTS

4.1 Migrations in Fresh Water

Salmo salar undertake migrations of varying complexity between estuarine, riverine, and lacustrine environments. The dynamics of these migrations (i.e. seasonality, magnitude, causal mechanisms, life history stages involved) are sufficiently unique to warrant separate treatment for movements into and out of the stream. The following sections are subdivided to describe movements at the lake/stream and stream/estuary confluences.

4.1.1 Emigration From Stream

4.1.1.1 Lakeward movements

Lakeward movements by salmon parr from the outlet streams occurred throughout both field seasons, from

early-May through late-November, at varying levels of intensity (Fig. 2). The magnitude of these movements was greatest during a 7-8 week period from mid-May to mid-July and during the spawning season in October and November. In 1982, 64.8% (n=166) and 25.0% (n=64) of the total parr movement into Wings Pond occurred during these spring (from commencement of trap operations to July 14) and autumn (October 1 - November 22) periods respectively. Spring and autumn figures for Bluehill Pond were 84.5% (n=109) and 5.4% (n=7) respectively. The 1983 spring period accounted for 91.7% (n=286) and 93.6% (n=176) of the total parr movements into Wings Pond and Bluehill Pond respectively.

Parr undertaking spring lakeward movements were predominantly one and two years of age (Fig. 3). A total of six underyearlings were captured in the upstream trap at Wings Pond (none were captured at Bluehill Pond) from May, 1982, to September, 1983. The shapes of the age frequency distributions are very similar between lake sites within each year. Length frequency distributions and corresponding mean values did not differ appreciably either between or within sampling sites (Fig. 4).

The trap at Wings Pond was checked twice daily on 53 occasions between May 15 and September 1, 1983, to determine the diel timing of lakeward movements. Initial trap checks

were conducted between 0700 and 1000h, followed by a second census 1 to 4 hours later. Most of the movement was diurnal (51%). Given the 7 to 11 hours of daylight following the second census, this percentage is a minimum value. The following counts of parr in the upstream trap on May 28 exemplify the diurnal aspect of lakeward movements: 0900h - 11 parr; 1155h - 16 parr; 1235h - 11 parr; 1300h - 12 parr; 1330h - 5 parr.

Environmental parameters (see page 25) explained only a small proportion (8.1%; $p>.05$) of the variance in daily parr movements into Bluehill Pond in both 1982 and 1983. Orders of variable addition (and thus importance) into the equation were as follows: 1982 - TEMPDIF, MINWATER, DEPTH, PRECIP; 1983 - MINWATER, DEPTH, TEMPDIF, PRECIP. DEPTH and TEMPDIF explained 27.8% ($p<.0001$) and 7.5% ($p=.043$) of the variance in daily parr movements into Wings Pond during 1982 and 1983 respectively. TEMPDIF had the higher partial correlation with the criterion variable in 1982 whereas DEPTH explained the greater variation in 1983. Low r^2 values (Table 4; significant values were effected by outliers) reiterate the negligible proportions of variation in parr movements explained by environmental factors.

Lakeward movements were directed and non-random. None of the parr moving into the lakes in 1983 had re-entered the

brook by October. In 1982, 2.6% and 20.0% of the parr moving into Wings and Bluehill Ponds respectively re-entered the outlet streams prior to the spawning period. Recaptures occurred during the first month of trap operations and can probably be attributed to the practice of returning parr to stream sections of moderate water velocity immediately above the entrance to the downstream trap. All recaptures were made within three days of clipping (81.5% within a single day) suggesting that parr were carried into the downstream trap by the current, possibly as a result of fatigue and/or disorientation. Parr were subsequently released directly into the lakes whereupon the recapture of lakeward migrating parr ceased.

Sexually mature males comprised 92.2% of the 64 parr moving into Wings Pond during the 1982 spawning season. The sex of the remaining 7.8% was unknown. Males were in a spending or spent condition (Jones 1959), and occurred in the following age frequencies: 1+ - 8.8%, 2+ - 23.5%, 3+ - 35.3%, 4+ - 29.4%, 5+ - 3.0%. Twenty-six spent males returned to Wings Pond the following spring.

Salmon kelt[4] moved into Wings Pond following the 1982 spawning season. There were two (55.0-56.0 cm FL) kelt in

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4. Spent or spawned-out anadromous salmon.

the outlet counting fence on June 6 and September 5 and three (49.2-55.7 cm FL) in the lake proper from September 18-24 in 1983. Kelt did not emigrate from Bluehill Pond.

4.1.1.2 Seaward movements

The downstream emigration of juvenile salmon from Wings Brook into Southwest Arm, the estuary, occurred throughout the 1982 and 1983 field seasons (Fig. 5). The emigration of salmon parr and smolt will be treated separately.

Parr

The number of parr moving into the estuary exceeded the sum total of lakeward migrating parr (Table 5). The bulk of this movement occurred during May and June (Fig. 5).

The lengths of parr moving into the estuary prior to the spawning season were normally distributed about means of 81 mm (1982) and 76 mm (1983) (Fig. 6). These fish were predominantly one and two years of age (Fig. 7). The length frequency distribution of parr emigrating throughout the 1982 spawning period had no obvious modal structure about a mean of 115 mm. A sample (58.2%; n_{tot}=122) of these autumn migrating parr were sexed and all were either ripe or spent males. A few of these males had left Wings (n=9) and Bluehill (n=3) Ponds within the previous month.

Parr movement was predominantly nocturnal. Afternoon trap checks accounted for less than one-quarter of all emigrating parr: 23.5% in 1982 and 20.6% in 1983.

Few parr moving into the estuary had left either of the lakes within the year. Only one parr from each of Wings (96 mm) and Bluehill (87 mm) Ponds entered the estuary prior to the 1982 spawning season. There were no such recaptures of lake-emigrating parr in 1983.

The variables DEPTH, MINWATER, MAXWATER, in descending order of explained variance, accounted for 40.3% ($p<.0001$) of the variance in daily parr movements into the estuary during 1982. The combination and ranking of MINWATER, MAXWATER, DEPTH comprised 59.2% ($p<.0001$) of the explained variance in 1983 parr movements. All three environmental parameters were positively correlated with daily parr movements.

Three female ouananiche entered the estuary in early November, 1982. All were spent. One (19.2 mm) had emigrated from Wings Pond, and the other two (27.7 and 31.2 mm) came from Bluehill Pond. It was apparent during handling of these fish that they were physically very weak.

Smolt

Migrations occurred primarily over 5-6 weeks in May and June with the bulk of the movement completed by July (Fig.

5). Maximum daily water temperatures ranged from 7.5 to 8.5°C when the migrations began. There was a small but substantive (8.1% of the total smolt production) autumnal emigration from early-September until late-November in 1982. There was no evidence of an autumnal run in 1983 although three smolt were enumerated at the counting fence on September 2.

The Wings Brook system produced 334 and 747 smolt in 1982 and 1983 respectively. Smolt entered the upper tributaries in large numbers from both Wings and Bluehill Ponds (Table 5). The number of smolt emigrating from the lakes exceeded the number entering the estuary in 1982. The lakes contributed 86.7% of the total smolt production of the system in 1983.

Smolt leaving Bluehill Pond were significantly ($p<.05$; Student's t-test) older (4.8 yr) than those leaving Wings Pond (4.0 yr). The ages of Wings Pond smolt were normally distributed whereas those from Bluehill Pond approached a platykurtic distribution with age classes 4 to 6 represented almost equally (Fig. 8). Smolt leaving Bluehill Pond averaged 202 mm FL in length as compared with 164 mm FL for those leaving Wings Pond (Fig. 9). The sex ratio of smolt sampled at the lower counting fence was skewed in favour of females by 6.4:1.0.

Ninety-eight smolt enumerated at the lower counting fence in 1983 had not been previously marked with a fin clip (indicative of lake origin). Their age distribution was as follows: 2 yr - 3.6%, 3 yr - 30.4%, 4 yr - 44.6%, 5 yr - 19.6%, 6 yr - 0.0%, 7 yr - 1.8%. The incidence of unmarked smolt decreased from 100% one day after the experiment began (May 6) to 21% on May 20 before reaching a rate of 16% averaged over the first two weeks of June. The first marked smolt was captured on May 11.

The majority of smolt entered the lower trap from 1600-0700h. A relatively small percentage of the smolt run (25.7% in 1982; 16.7% in 1983) was collected subsequent to the initial daily trap checks conducted at approximately 0800h.

4.1.2 Immigration Into Stream

4.1.2.1 Movement from lakes into stream

Parr movement into the outlet streams was infrequent during the spring and summer months, and involved few individuals (Figs. 10, 11). Peak periods of emigration were not evident as the relative intensity of these movements was uniformly low (Fig. 10). These fish ranged from 1-3 yr in

age and their length frequency distributions lacked a clearly defined peak (Fig. 11).

The apparent randomness associated with these intermittent pre-spawning emigrations contrasts sharply with the timing and magnitude of the autumnal movement of parr into the streams. Parr emigration from both lakes increased substantially during the second week of October, reaching peak magnitudes by the end of the month before tapering off during the second and third weeks of November (Fig. 10). Parr emigrating from Wings Pond included 764 sexually mature males (mean length - 13.4 cm [7.0-24.7 cm]) and 10 sexually mature females (mean length - 35.8 cm [15.3-52.3 cm]). The smallest female (15.3 cm; 40.9 g) contained 49 fully developed eggs. The spawning migration from Bluehill Pond included 301 mature males (mean length - 13.9 cm [7.6-22.7 cm]) and 10 mature females (mean length - 25.4 cm [22.0-31.2 cm]). Fin clipping data indicated that at least 6 (12.0-16.6 cm) of the 480 precociously mature males from Wings Pond migrated as smolt the following spring.

Smolt did not emigrate from Bluehill Pond in 1982 when water levels (measured at the counting fence) fell below 22.0 cm although smolt were leaving Wings Pond during the same time period. The number of smolt leaving Bluehill Pond increased 523% (relative to the 1982 total) upon removal of

the log jam in May, 1983. This compares with the 42% increase in smolt emigrating from Wings Pond over the same time period.

Smolt were collected at the lake outlets immediately after trap installation. Maximum daily stream water temperatures varied from 7.0-11.0°C. These emigrations were five weeks in duration. The runs were completed by June 30, 1982, and June 15, 1983. Timing of the smolt runs was similar between lakes within each year.

4.1.2.2 Movement from estuary into stream

The 1982 and 1983 upstream runs of Salmo salar into Wings Brook from Southwest Arm were each dominated by different life history stages. The few grilse that entered Wings Brook did so in 1982 when exceedingly few parr emigrated from the estuary (Table 5). Alternately, the substantive 1983 run was solely parr.

A maximum of 9 grilse and a minimum of 2 previous spawners migrated into Wings Brook in 1982. The migration began July 6 and ended September 22, and most adults had entered the brook by the third week of July. All but three fish had been scarred by gill nets.

The designation of grilse was originally made using a

length criterion considered to be reliable in separating one-sea-winter (1SW) salmon from multi-sea-winter (MSW) salmon. Adults less than or equal to 62 cm in fork length are classified as grilse (O'Connell et al. 1983). Fish length was approximated using a metre stick affixed to the bottom of the upstream trap. Using the length criterion alone, all returning adults were designated as grilse. However, scale analyses on five kelts showed that two of these fish (55.7 cm, 56.0 cm) had previously spawned (R.F. Burfitt and D. Riche, personal observation; Dept. Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld.). Thus, the length criterion is not an unequivocal method of identifying virgin 1SW salmon.

Anadromous adults did not migrate into Wings Brook in 1983. None were observed either below the counting fence or in the estuary.

Only eight parr moved from the estuary into the brook in 1982. They did so sporadically throughout the summer months.

A total of 89 parr entered the brook from the estuary between May 10 and September 21, 1983. In general, movement was high during the spring, low in the summer, and intermediate in intensity during the late summer/early autumn. Fifty percent of the movement occurred between June

12 and July 14. Parr moving prior to September averaged 69 mm in length (range 42-137 mm). A sample of 50 parr contained age classes 1+ (24%), 2+ (48%), and 3+ (18%). Ten of the 13 males entering the brook during September were sexually mature. These precocious males averaged 14.5 cm in length (range 11.0-17.6 cm). This is the first documentation of parr maturation under saline (18-20 ppt) conditions. An additional seven parr moving at this time were immature females.

4.2 Lake Collections of Salmo salar

Lake collections of Salmo salar (n=62) included both freshwater resident and anadromous migrant forms, each represented by various life history stages (Table 6).

Parr constituted 42% of the sample. The distal portion of the left pelvic fin on nine mature males was comprised of regenerative tissue disfigured into a form that would have arisen from an earlier fin clip. The only parr previously marked with a left pelvic fin clip were sexually mature males emigrating from Wings Pond during the autumn of 1982. Thus, 50% of the precocious male parr in this September 1983 sample had matured previously and had spawned in the outlet

stream.

The large standard deviation associated with the mean length of immature female parr (Table 6) can be attributed to the inclusion of a 26.9 cm fish (the others measured 9.3-9.5 cm). This particular female was aged at 6+ yr and her stomach contained 16 yearling smelt, Osmerus mordax.

Thirty-two Salmo salar were classified as "residual smolt". Power (1969: 40) originally coined the term to describe "...salmon smolts that have, for one reason or another, failed to migrate at the appropriate time". The gonads of two male residual smolt (18.7 cm; 21.4 cm, 75.0 g) were in a maturing state. The anterior portion of the testes measured 7-10 mm in width, corresponding to a developmental condition intermediate to Jones' (1959) stages II and III. By comparison, the testes of an immature male are about 1 mm wide (stage I) whereas those of a fully mature fish (stage V) completely fill the abdominal cavity.

The three kelt captured in Wings Pond were exceedingly thin. Each contained several (7-18) atretic eggs and scale analysis indicated a period of marine residence encompassing one winter.

4.3 Stream Collections of Juvenile Salmon

Length frequency distributions of salmon parr collected throughout Wings Brook are presented in Fig. 12. Underyearling parr have been excluded from the biomass and population density estimates.

The length frequency distribution of parr (4.1-12.5 cm FL) collected in Upper Wings Brook was significantly different from that of parr moving into Wings Pond (χ^2=483.3 > $\chi^2_{.05[16]}$=26.296). Biomass and population density were estimated to be 3.48 g m^{-2} and 0.80 individuals m^{-2} respectively.

The length frequency distribution of parr (5.1-11.5 cm FL) entering Bluehill Pond varied significantly from that of the parr collected from Bluehill Brook (χ^2=125.34 > $\chi^2_{.05[12]}$=21.026). Biomass and density estimates were 2.57 g m^{-2} and 0.40 individuals m^{-2} respectively.

The length-frequency distributions of parr measuring 4.1-12.5 cm collected at the lower brook sites were significantly different from one another (χ^2=29.256 > $\chi^2_{.05[16]}$=26.296) as was the distribution from the lower section with that of parr entering the estuary (χ^2=89.978 >

$\chi^2_{.05[16]}=26.296$). The upper and lower sections in lower Wings Brook had biomass/density estimates of 1.38 g m^{-2}/0.20 individuals m^{-2} and 2.62 g m^{-2}/0.40 individuals m^{-2} respectively.

Three residual smolt angled from the lower sections of Wings Brook in late-July possessed maturing gonads. The testes of a male (25.3 cm, 135.7 g) were at developmental stage II. The gonads of two females (22.3 cm, 79.7 g; 21.6 cm, 63.0 g) contained ova in stage 5 of exogenous vitellogenesis (van den Hurk and Peute 1979), i.e. these fish had the potential to spawn during the autumn. Classification of gonadal developmental stages was based upon macroscopic examination.

4.4 Growth

4.4.1 Scale Radius-Age Relationship

The growth rate of lacustrine and estuarine parr was significantly ($p<.0001$) greater than that of riverine parr (Table 7). Regression slopes within lacustrine and estuarine parr did not vary significantly from one another ($p>.05$), although such was not the case with their intercept values

($p<.05$).

Mean scale radius at the end of the first winter differed significantly ($F_s=25.12$; $p<0.01$) among mature, migrant, and riverine parr. Paired comparisons using least-significant differences between means indicated that mature male parr grew significantly ($p<0.05$) faster in their first year of life than either migrant or riverine parr. Migrant and riverine parr did not differ significantly in growth during their first year.

Growth rates of smolt did not differ significantly ($p>.05$) between Wings and Bluehill Ponds (Table 7).

4.4.2 Weight-Length Relationship

Summary statistics of the parr weight-length relationships are presented in Table 8. Regression slopes of lacustrine and riverine parr increased 4% and 11% respectively from 1982 to 1983. It is evident that the rates at which weight increases per unit length among the parr types are consistent with the pattern in the scale radius-age relationships.

Chapter 5

DISCUSSION

5.1 Impropriety of Classical Life History Accounts

The classical life history account of the Atlantic salmon incorporates, and in large part depends upon, the implicit assumptions that (1) movement during juvenile stages is limited (e.g. diel "micro-migrations") and infrequent prior to smoltification, and (2) the young remain in a fluviatile habitat throughout their freshwater phase of life. That is "...parr tend to stay near the area in which they were hatched..." (Jones 1959:28). The typical life history of Salmo salar can be summarized as follows: Atlantic salmon spawn in freshwater streams, the adults return to sea, the young remain in gravelly streams for 1 to 8 years, then descend to the sea to spend one or more years feeding and growing before returning to fresh water to spawn (Scott and Crossman 1973). This is the precept upon which

Atlantic salmon management programmes are conducted (e.g. Chadwick et al. 1978) and upon which life history theorists base their models (e.g. Schaffer and Elson 1975).

From the results of my study, it is evident that the foregoing assumptions concerning parr movements are clearly inappropriate for salmon populations inhabiting systems containing lacustrine habitat. Suitable estuarine habitat further complicates the scenario.

My first objective was to examine juvenile movements into and out of lakes. The freshwater migratory patterns described herein provide a foundation upon which the life history of Salmo salar in the Wings Brook system can be described. This model should embody the general life history framework of salmon inhabiting river/lake networks.

5.2 Life History of Atlantic Salmon in Wings Brook

5.2.1 Freshwater Phase

Anadromous and resident Salmo salar spawn in lake outlet streams[5] during late-October/early-November. The young emerge from the gravel in mid-June and remain in the stream for at least one year following which a proportion of all cohorts undertake upstream, lakeward movements. These predominantly diurnal movements occur over a 7-8 week period in the spring and are normally initiated by individuals in their second and third years of stream residence.

Juvenile Salmo salar remain in the lakes until smoltification (predominantly females) or maturation (usually males), whereupon they re-enter the outlet streams. Smolt emigrate from the lakes during the spring (May-June). Age at smoltification ranges from 2 to 7 years. Some smolt remain in the lakes and do not migrate. A small proportion of these residual smolt subsequently mature.

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5. The absence of spawning adults and redds around the lake peripheries and in the inlet streams during the autumn argues against the use of these areas as spawning sites.

Sexually mature S. salar enter the outlet streams in the autumn (October-November). Age at first maturity ranges from 1 (males) to 3 (females) years. Spent parr may remain in the stream and smoltify the following spring, or re-enter the lake either immediately after spawning or during the ensuing spring.

Anadromous adult salmon return to the brook in mid-July as grilse. These fish spend the intervening months prior to spawning either in deep pools within the river or in a lake. The majority of anadromous adults overwinter in the lakes and migrate to sea the following spring.

5.2.2 Estuarine Phase

Emigration of parr from Wings Brook into the estuary occurs primarily during the spring. Seasonal and diel (nocturnal) timing of this movement is characteristic of the smolt migration. Daily movements intensify during periods of increasing water levels and water temperature. Parr re-enter the stream during the late-spring and late-summer. Growth of estuarine parr exceeds that of riverine parr.

The majority of male parr ascending Wings Brook during late-summer are sexually mature. Presumably the mature males enter the stream to spawn in the upper tributaries.

Jones (1959) reported that ripe salmon parr migrate upstream immediately prior to and during the spawning season in the Welsh Dee.

Movement of Atlantic salmon parr into estuaries has been recorded throughout eastern Canada (Huntsman and Hoar 1939; Huntsman 1945; Saunders 1960; Power and Shooner 1966; Shears 1985), however, the significance and impetus for such movements are unknown. Chadwick (1982a) reported a coincident movement of parr and smolt during the spring in Western Arm Brook, Newfoundland. He attributed this movement to an annual "redistribution" of parr in a downstream direction. Huntsman (1945) quoted unpublished data of P.F. Elson's which indicated that freshets (periods of high discharge) may be important in stimulating this movement. Upstream movement from estuaries has been reported to occur in some Canadian Maritime rivers (Huntsman 1945; Saunders 1960).

5.3 Lakeward Migrations by Juvenile Atlantic Salmon

5.3.1 General Discussion

The movements of salmon parr between lentic and lotic

waters are migrations under the criteria set forth by Northcote (1978, 1984). He defined a migration to be directed (i.e. non-random) movements resulting in an alternation between two or more separate habitats, occurring with regular periodicity, and involving a large fraction of the population. Satisfying the third criterion is difficult because of the subjectivity in determining what constitutes a "large fraction of the population". Also, the proportion of a population actually undertaking specific migratory patterns may be entirely dependent upon the mechanisms motivating such movements.

Little documentation exists on movements by juvenile Atlantic salmon between lentic and lotic waters. Stuart (1957) noted that salmon parr accompany yearling and two-year-old brown trout, Salmo trutta, in a spring upstream migration from a Scottish reservoir into a feeder stream, returning to the reservoir in autumn. Salmon parr are known to move into small inlet streams from Lake Vangsvatnet, western Norway, during the spring and return to the lake to overwinter (B. Jonsson, personal communication in Northcote 1984). Pepper (1976) found a similarity in scale growth characteristics between smolt captured in the outlet of Salmon Pond, Newfoundland, and parr in the pond and in an inlet stream. He concluded that the inlet and pond served

as natal and rearing habitats respectively for juveniles prior to smoltification. Parr captured in Salmon Pond varied from 1 to 4 years in age. Pepper (1976) believed that lakeward movements were mediated by unfavourable stream conditions (e.g. high parr density, low water level, high water temperature) but he did not support this assertion with data.

Lakeward migrations are not uncommon among other juvenile salmonids. Rainbow trout, Salmo gairdneri, enter lakes from natal inlet streams shortly after emergence with most of the movement occurring at night (Northcote 1962, 1969). Upstream migrants are usually one or two years of age, and undertake diurnal movements during the spring and summer. Upstream movement is often positively correlated with changes in daily water temperature (Northcote 1969). Lakeward migrations by juvenile rainbow trout appear to be determined by both genetic and environmental factors (Kelso and Northcote 1981; Kelso et al. 1981). Cutthroat trout, S. clarki, migrate from lake outlets throughout the growing season following a stream residence of one or two years (Shapley 1961). Downstream migrants normally leave inlet streams as underyearlings (Benson 1960). Water temperature and photoperiod may have regulatory effects on cutthroat trout movements (Northcote 1969), but there is strong

evidence that lakeward migrations are largely dependent upon innately controlled rheotactic responses (Raleigh 1971; Raleigh and Chapman 1971; Bowler 1975). Juvenile brown trout, S. trutta, enter Loch Leven, Scotland, during the winter and early spring after one or two growing seasons in the inlet streams (Thorpe 1974). Downstream migrants at Lakes Windermere, England, and Ockesjön, Sweden, spend two or more years in the stream prior to migration (Gustafson 1949; Frost and Smyly 1952). Brown trout normally spend 3-4 years in outlet streams before migrating into Lakes Rensjön and Torrön, Sweden, from June through September (Runnström 1957). Seasonal and diel timing of upstream migrations appear to be regulated by increases in water temperature (Runnström 1957) although such factors have not been examined in detail. Movements by underyearling sockeye salmon, Oncorhynchus nerka, from outlet and inlet streams are typically diurnal and nocturnal respectively (McCart 1967). These movements are primarily under genetic control (Brannon 1967; Raleigh 1967, 1971).

5.3.2 Causal Mechanisms

Arguments used to explain freshwater migrations by other juvenile salmonids have limited applicability to

Atlantic salmon parr. Unlike the salmonid populations previously described, lakeward migrations by juvenile Salmo salar are not undertaken by all members of the population. Therefore, any hypothesis used to explain lakeward migrations must account for the differential responses of individual parr to the factor(s) inducing this movement. This would weaken arguments based upon the contention that parr migrate simply to avoid unfavourable environmental conditions (e.g. high water temperatures, low water levels) because such influences would presumably have an equivalent effect on all individuals.

Lakeward migrations by juvenile Atlantic salmon were not induced by physical environmental factors. These movements were at their minimum intensities when stream water temperatures and depths were at their respective maxima and minima. Water depth and rate of temperature increase can, however, act in concert to regulate lakeward movements.

Lakeward migrations could result from intra-specific competition for limited stream habitat suitable for the establishment of feeding territories. Chapman (1962) hypothesized that agonistic behaviour associated with competition for food resources was a primary factor inducing the downstream movement of underyearling coho salmon,

Oncorhynchus kisutch. Symons (1968, 1971) reported increased aggression among Atlantic salmon parr with limited food resources. Gibson and Dickson (1984) attributed increased growth among juvenile Salmo salar to reduced intra-specific competition under conditions of low parr density and abundant food.

The hypothesis that lakeward migrations are mediated through intra-specific competition is rejected for several reasons. First, subordinate individuals are normally displaced in a downstream direction following agonistic encounters with dominant fish (Chapman 1962; Gibson 1981; McNicol and Noakes 1981). Second, juvenile Atlantic salmon feed primarily on stream invertebrate drift (Wankowski and Thorpe 1979a). Displacement of a subordinate parr in an upstream direction would be disadvantageous to the dominant parr if the subordinate was given the opportunity to consume a food particle before it drifted toward the dominant. Also the upstream sections of outlet streams should be the preferred sites for feeding territories because drift invertebrate biomass suitable as food for parr increases with proximity to lake outlets (Gibson and Galbraith 1975). Third, competitve displacement of subordinate parr should be greatest when food supply is limiting (Symons 1971), yet lakeward migrations occur when food resources are at their

greatest abundance (Gibson and Galbraith 1975). Furthermore, since dominance is size-related (Kalleberg 1958; Symons 1968; Jenkins 1969), one would expect lakeward migrants to be comprised of the smaller individuals within and/or between age classes if competition is important. My data do not support this prediction. Growth rates of migrant parr in their first year of life did not differ significantly from those of riverine parr. Finally, movement in an upstream direction (active) is energetically more demanding than downstream drift (passive) (Beamish 1978). This is illustrated in Bluehill Brook where parr must negotiate a short series of rapids and relatively high (5-10 cm) vertical falls before entering Bluehill Pond. Such behaviour is indicative of a non-random, intended movement rather than a haphazard, unintended displacement.

Salmon parr may be attracted to high densities of drift invertebrates in the lake effluent and enter the lake in response to this food stimulus. However, there is little evidence of such a response among riverine salmonids. Slaney (1972) found lakeward migration of juvenile rainbow trout and drift density to be inversely related. Similarly, the emigration rate of rainbow trout fry from experimental channels was low when prey density within the channels was high (Slaney and Northcote 1974). Wankowski and Thorpe

(1979a,b) thought that as optimal food particle size for growth increases, salmon parr should select their feeding habitats accordingly. Thus, large parr would move into the lake waters to exploit larger lacustrine food particles (e.g. yearling smelt). However, parr undertaking lakeward movements in the Wings Brook system were not significantly larger than those remaining in the stream. Furthermore, Thonney (1984) found prey size and width of gape to be unrelated for juvenile salmon and brook char in Wings Brook.

Lakeward movements may simply be an extension of general stream dispersal movements by salmon parr in the spring. The magnitude of this movement would then be density-dependent. Salmonid fry typically disperse both upstream and downstream from their nest site following emergence (Godin 1982). Stocking experiments have provided circumstantial evidence that older parr may undertake similar "re-distributional" movements (MacCrimmon 1954; Solomon and Templeton 1976).

The co-occurrence of lakeward migrant and stream resident parr might be explained as an evolutionary phenomenon using game theory (Maynard Smith 1974, 1982). Game theory considers evolution at the phenotypic level when the fitnesses of particular phenotypes, or strategies, depend on their frequencies in the population. In this

context, stream residency and lakeward migration can be considered to be two different strategies employed by salmon parr. If the two strategies provide equal fitness at the individual level and cannot be invaded by an alternative strategy, then they can exist as a mixed Evolutionarily Stable Strategy (mESS) (Maynard Smith 1982).

One serious difficulty arises, however, when explaining lakeward migrations in a game theoretic context. For the two strategies (stream residency, lakeward migration) to exist in an evolutionarily stable state, the fitnesses of each must be equal (Maynard Smith 1982). Data collected at Wings Brook indicate that the probability of migrating to and maturing at sea is much higher for lacustrine parr than it is for riverine parr. This would imply unequal fitness between phenotypes unless (1) all riverine parr mature in fresh water and (2) their smaller size at maturity does not hinder their reproductive success. Given that these prerequisites for equal fitness seem unrealistic, the two strategies may not have evolved as mixed ESS's.

This difficulty can be reconciled if the problem is viewed at the individual level and if migrations at the parr stage to the lakes and estuary are thought of as alternate reproductive tactics. Subordinate reproductive tactics can evolve to provide animals with the opportunity to make the

Best of a Bad Situation (BBS) (Gross 1984). That is, migrations into lakes and estuaries can be evolutionarily stable despite the unequal fitness of such tactics (Gross 1984).

The argument can be further developed as follows. The riverine environment is poor in terms of growth and survival to smolt size (12-15 cm). Given that size can be positively correlated with reproductive fitness (increased fecundity, increased survival, superior competitive advantage during spawning), a proportion of the parr population should adopt behaviours that will enhance growth and survival. Both the estuary and lakes provide conditions for increased growth. The movement data indicate, however, that survival to sexual maturity in the estuarine environment is much lower than in the lakes. Estuarine parr may be more susceptible to predation because of their smaller (relative to smolt) size. In this context, lakes seem to be the best habitat in terms of reproductive fitness. If parr must emigrate from the stream in order to reduce size-specific mortality and increase growth, then movements into the lakes and estuary represent alternate reproductive tactics of which the latter is the subordinate. The opportunity to migrate into lakes would be dependent upon an individual's proximity to that lake, a location determined by random dispersal following

emergence from the gravel. It is assumed then that all individuals belong to the same gene pool and have equal expected fitnesses at birth. Thus the alternate tactics of estuarine and lakeward migrations may have evolved as a BBS and are evolutionarily stable. Gross (1984) interpreted the reproductive strategy of maintaining dwarf and "normal" phenotypes in Arctic char populations (see Jonsson and Hindar 1982) as having evolved as a BBS.

My research supports the thesis that lakeward migrations by juvenile Atlantic salmon are innately controlled but environmentally regulated. This interpretation has been invoked to explain these movements among other salmonids (see page 54). The adaptive significance of these migrations is exemplified by the increased growth and survival (i.e. fitness) experienced by lacustrine parr relative to riverine parr. A frequency-dependent mechanism operating at the phenotypic level could account for the fact that only a portion of the population migrates.

5.4 Management Considerations

Assessing the relative importance of riverine and

lacustrine habitat to Atlantic salmon production is necessary for successful management of populations inhabiting river/lake systems. The following discussion incorporates the second objective of this thesis g.e., to determine the importance of lacustrine habitat to Atlantic salmon production.

5.4.1 Smolt Biomass in Lacustrine Habitat

Smolt production in the Wings Brook system occurred almost entirely within the lakes. Biomass estimates for Wings and Bluehill Ponds were 145.1 g ha^{-1} and 93.5 g ha^{-1} respectively in 1983. Minimum smolt density estimates ranged from 2.66 smolt ha^{-1} (1982) and 3.82 smolt ha^{-1} (1983) in Wings Pond to 1.46 smolt ha^{-1} (1983) in Bluehill Pond. Chadwick and Green (unpublished MS) calculated smolt density in a small (7.1 ha) pond of the Western Arm Brook system to be 0.28 smolt ha^{-1} in 1978. Indirect calculations suggest that two-thirds of the smolt production in Western Arm Brook occurs within lacustrine habitat (Chadwick and Green loc. cit.).

The suitability of lakes as juvenile salmon habitat is exemplified by the increased growth rates experienced by

lacustrine parr relative to riverine parr. Abundant food resources coupled with reduced competitive interactions among parr are probably the main factors contributing to this enhanced growth. Pepper (1976) reported growth rates among parr inhabiting a lake in central Newfoundland to be superior to those of parr in an inlet stream. Growth rates of salmon parr stocked into lakes in the British Isles exceed those of their riverine counterparts (Harris 1973; Pedley and Jones 1978).

5.4.2 The Importance of Lakes as Overwintering Habitat

The relative production of smolt in the riverine and lacustrine environments in the Wings Brook system emphasizes the importance of lakes as overwintering habitat. The majority of smolt originate in the lakes yet the proportion of the population initially entering the lakes as parr is relatively small. This suggests that survival to the smolt stage is much higher in the lakes than it is in the stream. This may be due to a lack of suitable riverine overwintering habitat for large parr and pre-smolts. Deep pools comprise only a small proportion (13.5%) of the total stream area of Wings Brook. While it has been demonstrated that juvenile salmon will overwinter in sheltered chambers within the

stream substrate (Smirnov et al. 1976; Gibson 1978; Rimmer et al. 1983) it is not clear that large parr or pre-smolts behave similarly. The autumnal emigrations of large parr and pre-smolts in many rivers (Calderwood 1906; Saunders 1960, 1976; Meister 1962; Pyefinch and Mills 1963; Youngson et al. 1983) suggest otherwise.

Riddell and Leggett (1981) hypothesized that the autumnal emigration of large parr from Rocky Brook into the main stem of the Southwest Miramichi River was due in part to the high rate of energy loss that these fish would incur if they remained in the relatively small brook during the winter. The relative lack of deep water in Wings Brook may result in high mortality among large parr and pre-smolt during severe winters. Increases in parr mortality rates with size have been reported (Elson 1962; Myers 1984). Autumnal lakeward movements by juvenile Atlantic salmon have been previously observed (Stuart 1957; B. Jonsson loc. cit.). Other juvenile salmonids known to overwinter in lakes include coho salmon, Oncorhynchus kisutch, cutthroat trout, and rainbow trout (Cederholm and Scarlett 1982; Peterson 1982).

5.4.3 Inhibitory Effect of Lakes on Smolt Migration

The inhibitory effect of lakes on smolt migration has been previously documented. Harris (1973) noted that 4.5-41.8% of the smolt stocked into Loch Kinardochy, Scotland, failed to migrate to sea. These fish subsequently matured and remained in fresh water. Failure to migrate may be due in part to weak directional cues resulting from reduced lacustrine water currents (Harris 1978) or low outlet discharge rates (Jones and Evans 1962; Harris 1973). Smirnov (1979; cited in Chernitskiy and Loenko 1984) concurred with Ward (1932) in hypothesizing that rapid warming of the epilimnion may establish a thermal barrier to smolt migration, compelling smolt to move into deeper, cooler waters. Ricker (1940) believed that maturation and reproduction of residual sockeye salmon smolt may have been responsible for the formation of kokanee, the freshwater resident form of Oncorhynchus nerka. "Desmoltification" and subsequent maturation of Atlantic salmon smolt physically retained in freshwater have been widely reported (Day 1880-1884; Berg 1948; Evropeytseva 1962; Lundqvist and Fridberg 1982).

Several residual smolt captured in the Wings Brook system possessed gonads in a sexually maturing state. The contention that these fish smoltified during the preceding spring is supported by both observational and experimental

evidence. Body colouration (silvery in appearance, fin margins blackened) and morphology (slim, streamlined form) were those characteristic of a smolt (Hoar 1976; Wedemeyer et al. 1980). Smolt retained in fresh water do not lose their silvery lustre until late-autumn (Malikova 1959). Parr marks were rarely discernable among these fish. The probability that these fish were undergoing smoltification in preparation for a seaward migration the following spring is low. Thickening of the scale and skin purine layers that produces the silvery body colouration normally occurs 3-4 months prior to smoltification (Johnston and Eales 1967; Eriksson and Lundqvist 1982), although there may be exceptions in northern rivers (Power 1969).

5.5 Sympatry of Anadromous and Non-anadromous Salmo salar

Lakes are the dominant feature of watersheds supporting both anadromous and non-anadromous Salmo salar (e.g. Leggett and Power 1969; Riley et al. 1984). By evaluating the consequences of adopting different migratory strategies, some insight can be gained into how anadromous and non-anadromous forms may have originated within a species,

and how these forms may persist as two alternative phenotypes in a single population. This addresses my third objective i.e., to identify mechanisms allowing for the sympatry of anadromous and resident S. salar.

5.5.1 Genetic Relatedness

There is good reason to believe that the ouananiche are not genetically distinct from anadromous salmon in the Wings Brook system. Both forms spawn in the outlet streams, thus reducing the probability of spatial reproductive isolation and increasing the likelihood of interbreeding. There are no behavioural isolating mechanisms preventing reproductive isolation between ouananiche and anadromous salmon (Hutchings and Myers, in prep.). Hybrid offspring will mature and successfully reproduce (Sutterlin and Maclean 1984). There were no significant differences in the mtDNA sequences of parr collected from Wings Pond and lower Wings Brook (U. Gyllensten, Department of Genetics, University of Stockholm, Stockholm, Sweden; personal communication). If lacustrine and riverine parr in the Wings Brook system were representative of the resident and anadromous forms, then the mtDNA results would not have been expected if the forms were genetically distinct. There is some indication that

ouananiche and anadromous salmon in the North Arm River, an expansive network of lakes and streams in eastern Newfoundland, may be reproductively isolated (Couturier, Clarke, and Sutterlin, in prep.). The genetic relatedness between sympatric forms of salmonids is probably a function of the spatial separation and diversification of suitable spawning habitat within a given river/lake system. Rice (1984) postulated that reproductive isolation between habitat specialists can evolve if disruptive selection is applied to habitat preference.

5.5.2 Mechanisms of Sympatry

Do anadromous and non-anadromous salmon persist as two alternate phenotypes through time, or is their present co-occurrence a transient phenomenon? I consider four mechanisms by which ouananiche can co-exist with anadromous salmon in the Wings Brook system.

(1) The argument most widely invoked to explain the existence of resident salmonids contends that non-anadromous forms differentiated from an anadromous ancestor during the Wisconsin glaciation (8000 y BP). Minor advances and retreats of glacial fronts in concert with isostatic rebound geographically isolated these forms for relatively brief

periods of time, resulting in their obligatory adoption of a life cycle in fresh water within lakes (Behnke 1972). However, this explanation can only account for the origin of resident salmon in landlocked systems. It does not explain the persistence of ouananiche in lakes such as Wings and Bluehill Ponds. Unless the fitnesses[6] of anadromous and resident forms are equal, the less fit phenotype would have been selected against when connection to the sea had been re-established.

(2) The hypothesis that ouananiche could be initiated and maintained through the reproduction of residual smolt (Power 1958, 1969) will account for residency in a small proportion of a population. However, it does not provide a legitimate mechanism for the persistence of sympatric anadromous and non-anadromous forms because adoption of a freshwater existence by residual smolt is obligatory and non-adaptational. Again, if the fitness of residual Salmo salar does not equal that of anadromous salmon, then the non-anadromous form will not persist.

(3) Changes in the non-anadromous proportion of a

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6. Fitness is the relative competitive ability of a given phenotype expressed as the average number of surviving progeny of one phenotype compared with the average number of surviving progeny of competing phenotypes.

population can be effected through habitat disturbance and overfishing, i.e. human interference. The log jam located at the mouth of Bluehill Pond prevented smolt from leaving the lakes at low water levels. These fish became isolated within the lakes, effectively existing as ouananiche. There is evidence that increased fishing pressure can induce larger proportions of a population to mature in fresh water if suitable conditions for growth and survival (e.g. lakes) exist (Gibson 1978b; Myers 1983). The sympatry of anadromous and non-anadromous salmon under these circumstances would then be a transient phenomenon.

(4) Residency and anadromy may persist because they are alternative evolutionarily stable strategies or ESS's (Maynard Smith 1974, 1982). This can occur if the fitnesses of individuals adopting each strategy are, on average, equal, and if a frequency-dependent mechanism maintains a constant proportion of both phenotypes (Gross 1984). The frequency-dependent mechanism can operate at the individual level, such that anadromy and residency represent alternative ESS's within a population, or at the population level, such that two non-interbreeding populations exist each of which manifests itself as either ouananiche or anadromous salmon. The equilibrium frequency is determined by the environmental properties or behaviours governing the

frequency-dependent success of the phenotypes (Gross 1984). For example, if frequency-dependence operates through the availability of lacustrine habitat, then systems differing in lake abundance will have correspondingly different equilibrium frequencies of ouananiche and anadromous salmon.

In summary, the first two arguments do not explain the co-occurrence of anadromous and non-anadromous salmon in the Wings Brook system. The third explanation accounts for their co-occurrence on a short-term basis. Only the fourth mechanism accounts for their persistence on a long-term basis.

5.6 Future Considerations

The Salmonidae are an appropriate group in which to study life history evolution. The sympatry of anadromous and resident forms is an excellent example of life history variation in natural populations. Hutchings and Morris (1985) predicted that behaviour and life history traits should co-evolve to form optimal strategies which convey selective advantage under specific environmental contexts. The relationship between environmental complexity and

phenotypic plasticity could be examined by studying sympatric forms in a variety of river/lake systems representing a broad spectrum of geographical (niche) diversity.

The game theoretic hypotheses concerning lakeward migrations could be evaluated by comparing the relative fitness of estuarine, riverine, and lacustrine parr. Jonsson and Hindar (1982) consider $l_x f_x$ to be an appropriate measure of fitness, where l_x is the age-specific survival rate and f_x represents age-specific production of female zygotes. Population estimates of Salmo salar in the lakes and river would be necessary to calculate survival. The effect of parr migrations on the relative fitness of juvenile salmon could be modelled by varying the proportions of the stream population that enter the lakes and the estuary, and monitoring resultant $l_x f_x$ values. The conditions under which such migrations are evolutionarily stable could then be assessed. Gross (1985) estimated the lifetime fitness of male coho salmon as the product of survival to maturity, breeding lifespan, and mating success.

Finally, the overwhelming importance of lakes to Atlantic salmon production in Newfoundland is a fact which

should be incorporated into currently stream-oriented management practices. Stocking of lakes with parr has the potential to significantly increase the size of salmon populations throughout the island. There is clearly a need for further investigations on salmon populations inhabiting river/lake systems.

Chapter 6

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TABLE 1. Physical characteristics of Wings Brook, Newfoundland, and its tributaries.

Section	Axial length (m)	Mean width (m)	Total area (m^2)	%riffle	%run	%pool	%falls	%rapids
Wings Brook	1030	5.3	5437	91.0	7.8	0.3	0.0	0.8
Upper Wings Brook	870	4.1	3558	83.6	15.1	0.6	0.0	0.7
Bluehill Brook	1545	3.3	5086	78.8	19.0	0.0	2.2	0.0

TABLE 2. Water chemical parameters measured throughout the Wings Brook system.

Chemical[1] parameter	Lower Wings Brook	Wings Pond	Bluehill Pond	n
pH	6.48±0.32	6.17±0.30	6.45±0.20	16
	6.28±0.13	6.28±0.48	6.37±0.13	3
Calcium (mgl^{-1})	2.0±0.2	1.7±0.1	2.5±0.2	16
	2.3±0.2	1.7±0.1	2.5±0.1	3
Nitrate (mgl^{-1})	0.007±0.005	0.016±0.012	0.009±0.005	16
	0.007±0.004	0.007±0.004	0.005±0.002	3
Total phosphorus (mgl^{-1})	0.045±0.026	0.030±0.015	0.019±0.013	16
	0.007±0.003	0.011±0.007	0.029±0.034	3
Sulphate (mgl^{-1})	1.5±0.3	1.6±0.3	1.6±0.3	16
	2.2±0.3	1.9±0.1	1.9±0.2	3
Chloride (ppm)	6.1±0.3	6.2±0.3	5.6±0.2	16
Hardness (ppm $CaCO_3$)	8.2±1.2	7.6±1.3	8.8±0.9	16
Specific conductivity (umhos@25°C)	36.5±1.5	33.1±1.3	36.5±0.7	16
Total alkalinity (mgl^{-1} $CaCO_3$)	4.9±0.7	2.8±0.3	5.3±0.4	16
Turbidity (JTU)	1.37±0.32	1.44±0.46	1.08±0.26	16
Total dissolved solids (mgl^{-1})	---	25.2±18.3	22.1±13.6	8

[1]year of measurement: upper value - 1982, lower value - 1983, otherwise 1982

TABLE 3. Dates of counting fence operations on the Wings Brook system.

Station	Trap section	Dates of operation
Lower Wings Brook	upstream	July 2 - November 23, 1982 May 4 - September 29, 1983
	downstream	May 21 - November 23, 1982 May 4 - September 29, 1983
Wings Pond	upstream	June 9 - November 23, 1982 May 5 - September 28, 1983
	downstream	May 21 - November 23, 1982 May 5 - September 28, 1983
Bluehill Pond	upstream	June 1 - November 22, 1982 May 5 - September 28, 1983
	downstream	May 28 - November 22, 1982 May 5 - September 28, 1983

TABLE 4. Variation in daily parr movements into lakes explained by five environmental factors.

	Wings Pond		Bluehill Pond	
	1982	1983	1982	1983
Parameter	(r^2)	(r^2)	(r^2)	(r^2)
MAXWATER	.009	.017	.001	.093*
MINWATER	.005	.000	.040	.157*
DEPTH	.121*	.008	.017	.033
PRECIP	.004	.011	.010	.028
TEMPDIF	.131*	.071	.076*	.006

*significant at α = .05

TABLE 5. Total numbers of fish moving through the Wings Brook counting fences.

Station	Atlantic salmon smolt	parr	grilse	kelt	ouananiche	Brook char	American eel	Rainbow smelt	Arctic char	Threespine stickleback
1982										
Lower Wings Brook										
UP	3	8	11	0	0	42	0	0	0	3
DOWN	334	661	0	0	3	659	74	4682	0	24
Wings Pond										
UP	5	259	1	0	1	89	1	0	0	1
DOWN	322	840	1	0	10	289	48	132	0	124
Bluehill Pond										
UP	1	119	1	0	0	26	0	0	0	0
DOWN	30	368	1	0	9	316	18	19	2	0
1983										
Lower Wings Brook										
UP	0	89	0	0	0	419	0	0	0	9
DOWN	433	670	0	1	0	569	89	359	0	6
Wings Pond										
UP	8	319	0	0	0	54	0	0	0	0
DOWN	462	32	0	2	0	132	15	6	0	19
Bluehill Pond										
UP	1	188	0	0	0	43	0	0	0	0
DOWN	187	70	0	0	5	128	22	165	4	0

TABLE 6. Length (cm) and reproductive state of Salmo salar in Wings Pond, September, 1983.

Life history stage	MALE		FEMALE		
	Immature	Mature	Immature	Mature	Spent
Parr	8.9±0.3 (n=2)	16.6±2.5* (n=9)	13.8±7.6 (n=4)	19.5 (n=1)	---
		18.3±2.9 (n=9)			
Residual smolt	17.2±2.4 (n=7)	20.0±1.3 (n=2)	18.0±3.0 (n=23)	---	---
Kelt	---	---	---	---	51.4±3.0 (n=3)

*regenerated left pelvic fin

TABLE 7. Summary of the scale radius (y) - age (x) regressions for parr and smolt in the Wings Brook system; equations are of the form $y = mx + b$.

Classification	Slope (m)	Intercept (b)	r^2	n
Lacustrine parr	11.41	-0.57	0.63	421
Riverine parr	7.73	-2.95	0.58	286
Estuarine parr	13.36	-9.52	0.57	52
Wings Pond smolt	5.13	23.19	0.21	157
Bluehill smolt	5.54	31.19	0.27	103

TABLE 8. Summary of the $\log_{10}$ weight (y) - $\log_{10}$ length (x) regressions for parr in the Wings Brook system; equations are of the form $y = mx + b$.

Parr classification		Slope (m)	Intercept (b)	r^2	n
Lacustrine	1982	3.03	-5.03	0.99	39
	1983	3.15	-5.29	0.98	75
Riverine					
	1982	2.90	-4.76	0.90	534
	1983	3.21	-5.39	0.96	807
Spawning					
	1982	2.80	-4.54	0.96	686
Estuarine					
	1983	3.11	-5.19	0.97	68
Overall		3.00	-4.96	0.96	2209

TABLE 9. Mean lengths, in cm (range in parentheses), of Anguilla rostrata, Osmerus mordax, and Gasterosteus aculeatus moving downstream in Wings Brook.

Station		Anguilla rostrata	Osmerus mordax	Gasterosteus aculeatus
Lower Wings Brook				
	1982	66.8 (30.0-80.0) (n=74)	15.1 (12.5-23.9) (n=135)	5.7 (4.6-6.8) (n=24)
	1983	58.0 (30.0-75.0) (n=8)	17.0 (13.6-26.6) (n=135)	6.2 (4.9-8.9) (n=6)
Wings Pond				
	1982	77.7 (36.0-80.0) (n=47)	8.9 (7.6-21.3) (n=54)	4.9 (3.3-6.5) (n=105)
	1983	59.0 (30.0-75.0) (n=14)	8.2 (7.5-8.7) (n=6)	5.2 (4.2-5.9) (n=18)
Bluehill Pond				
	1982	65.4 (40.0-100.0) (n=18)	8.9 (7.5-9.7) (n=19)	
	1983	83.3 (70.0-95.0) (n=3)	8.1 (5.9-9.7) (n=90)	

Figure 1: Map of the Wings Brook system, Bonavista Bay, Newfoundland.

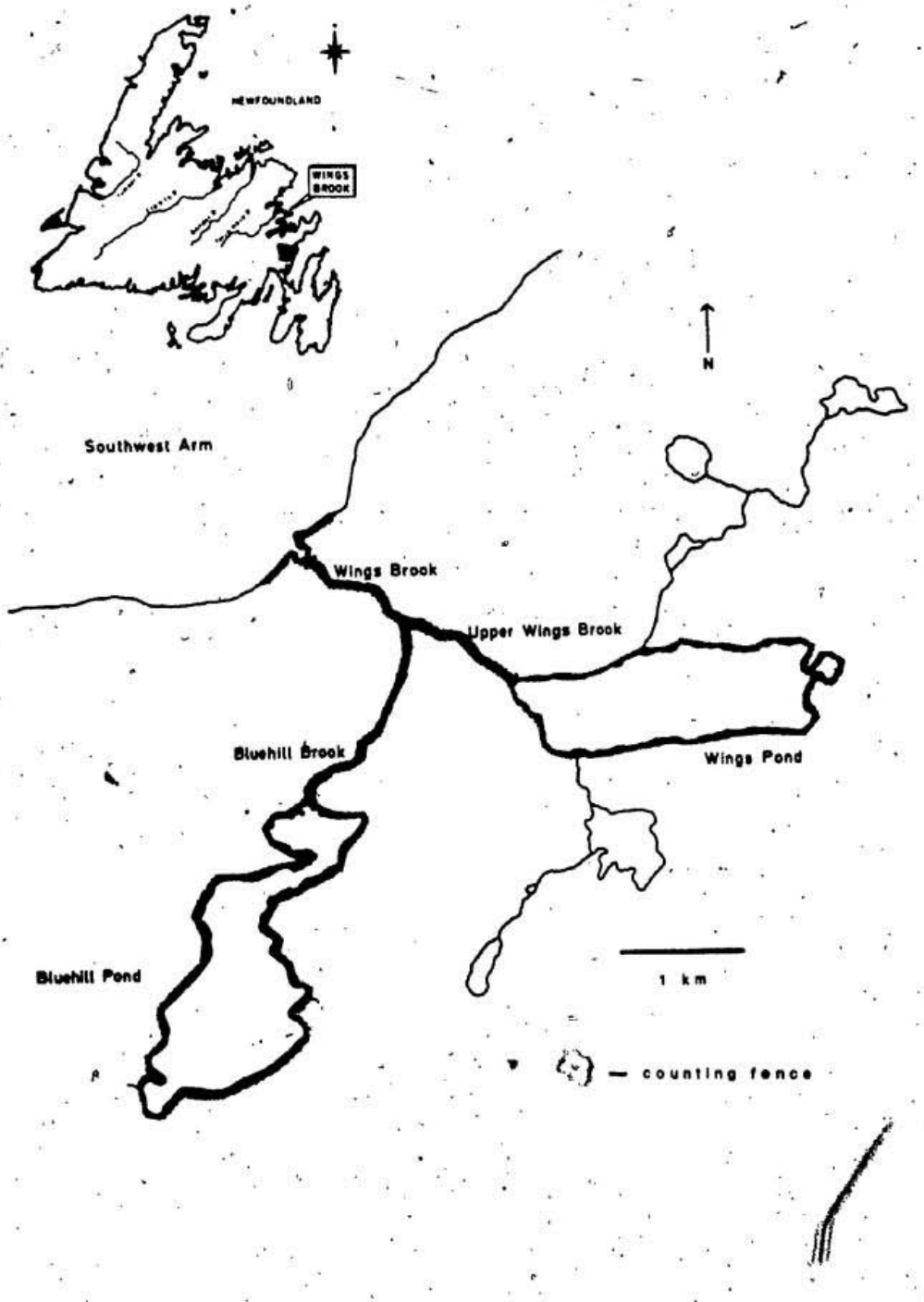

NEWFOUNDLAND
WINGS BROOK
N
Southwest Arm
Wings Brook
Upper Wings Brook
Bluehill Brook
Wings Pond
Bluehill Pond
1 km
— counting fence

Figure 2: Chronology of lakeward movements by salmon parr into Wings and Bluehill Ponds. Arrows indicate dates of trap installation and removal.

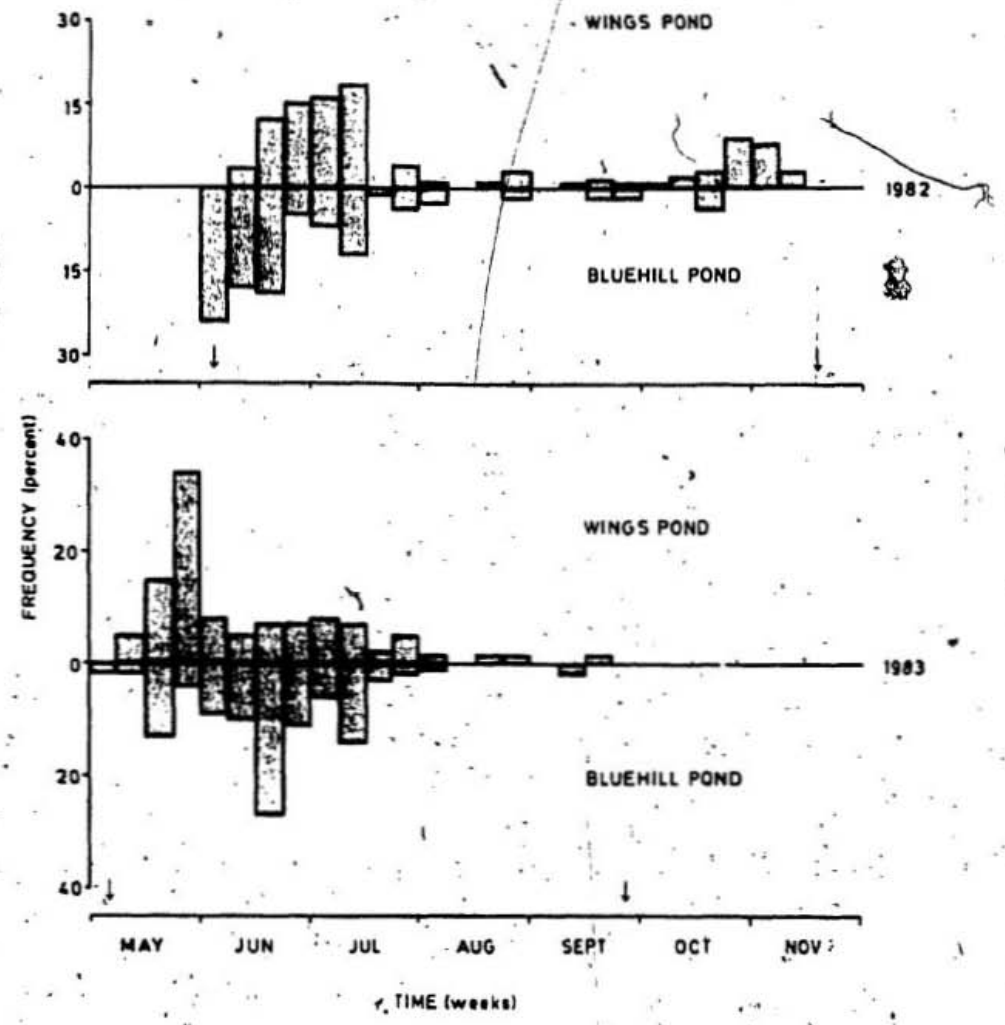

WINGS POND
30
15
0
15
30
1982
BLUEHILL POND
FREQUENCY (percent)
40
20
0
20
40
WINGS POND
1983
BLUEHILL POND
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
TIME (weeks)

Figure 3: Age-frequency distributions of salmon parr moving into Wings and Bluehill Ponds prior to the spawning season.

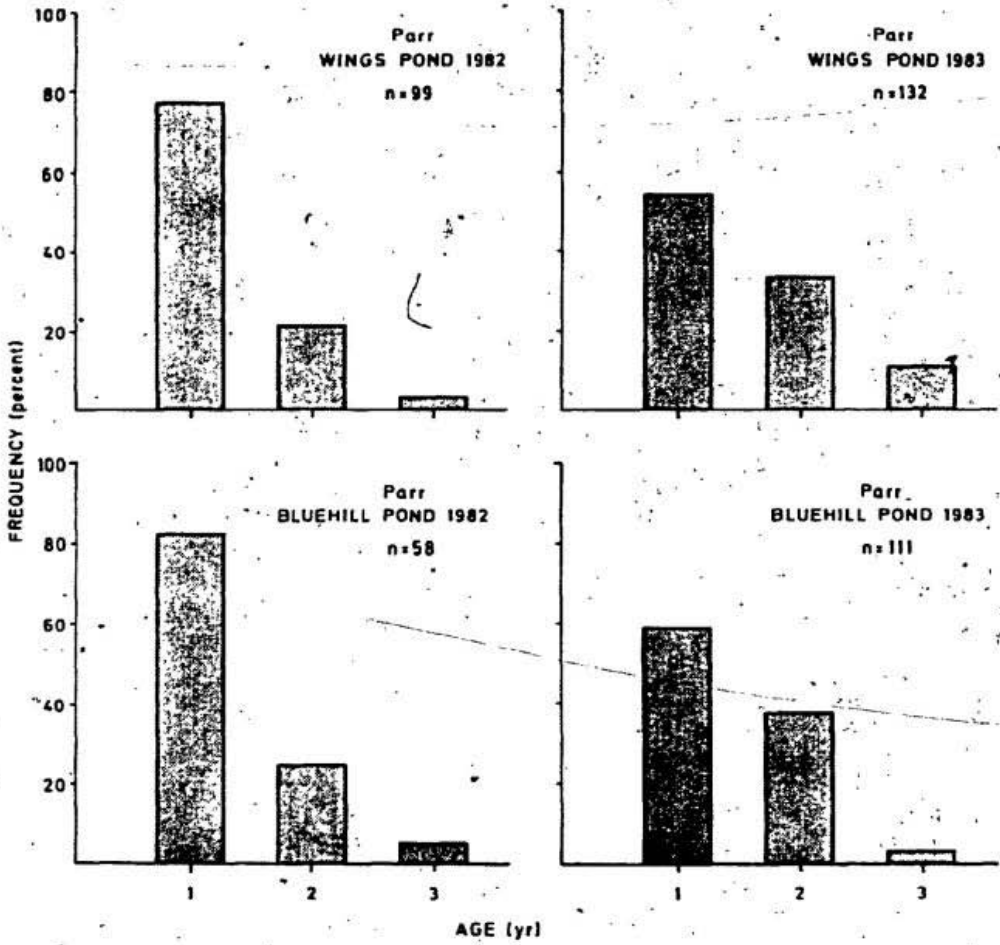
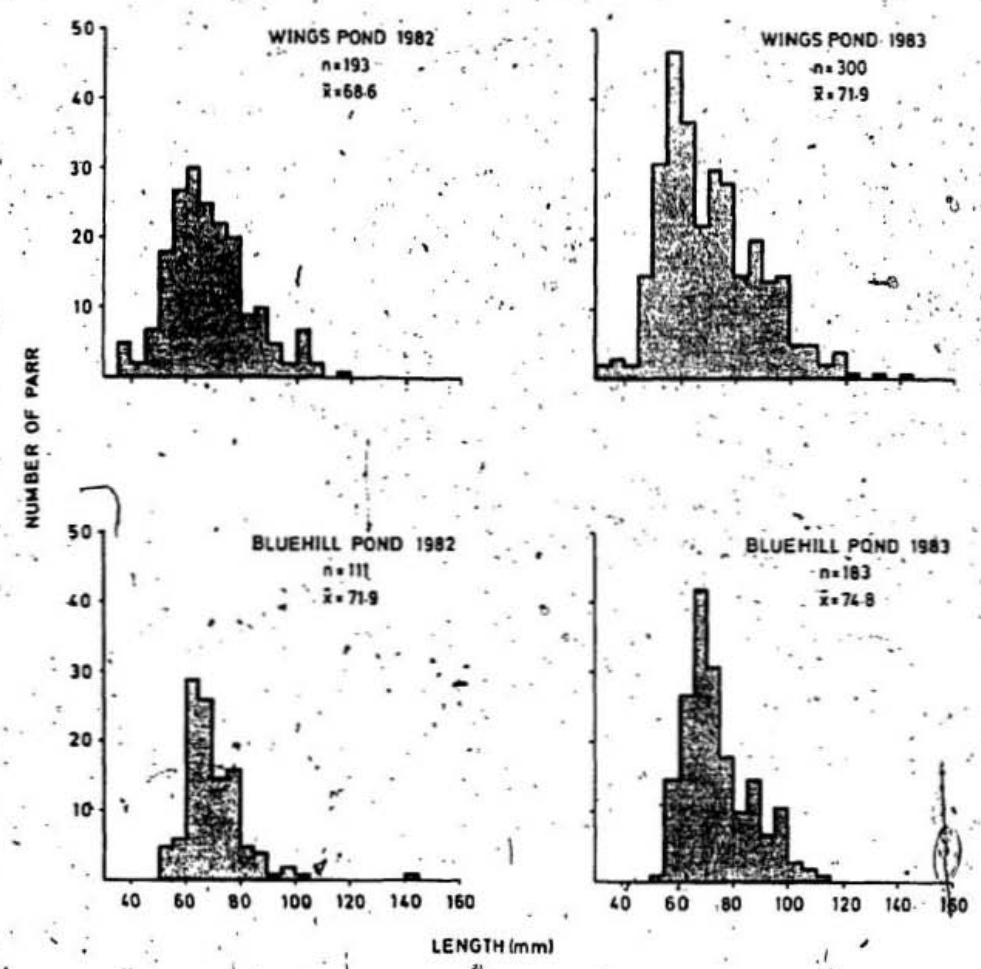

Parr
WINGS POND 1982
n=99
Parr
WINGS POND 1983
n=132
Parr
BLUEHILL POND 1982
n=58
Parr
BLUEHILL POND 1983
n=111
FREQUENCY (percent)
100
80
60
40
20
1
2
3
AGE (yr)

Figure 4: Length-frequency distributions of salmon parr moving into Wings and Bluehill Ponds prior to the spawning season.


WINGS POND 1982
n=193
x̄=68.6
WINGS POND 1983
n=300
x̄=71.9
BLUEHILL POND 1982
n=111
x̄=71.9
BLUEHILL POND 1983
n=183
x̄=74.8
NUMBER OF PARR
LENGTH (mm)
10
20
30
40
50
40
60
80
100
120
140
160

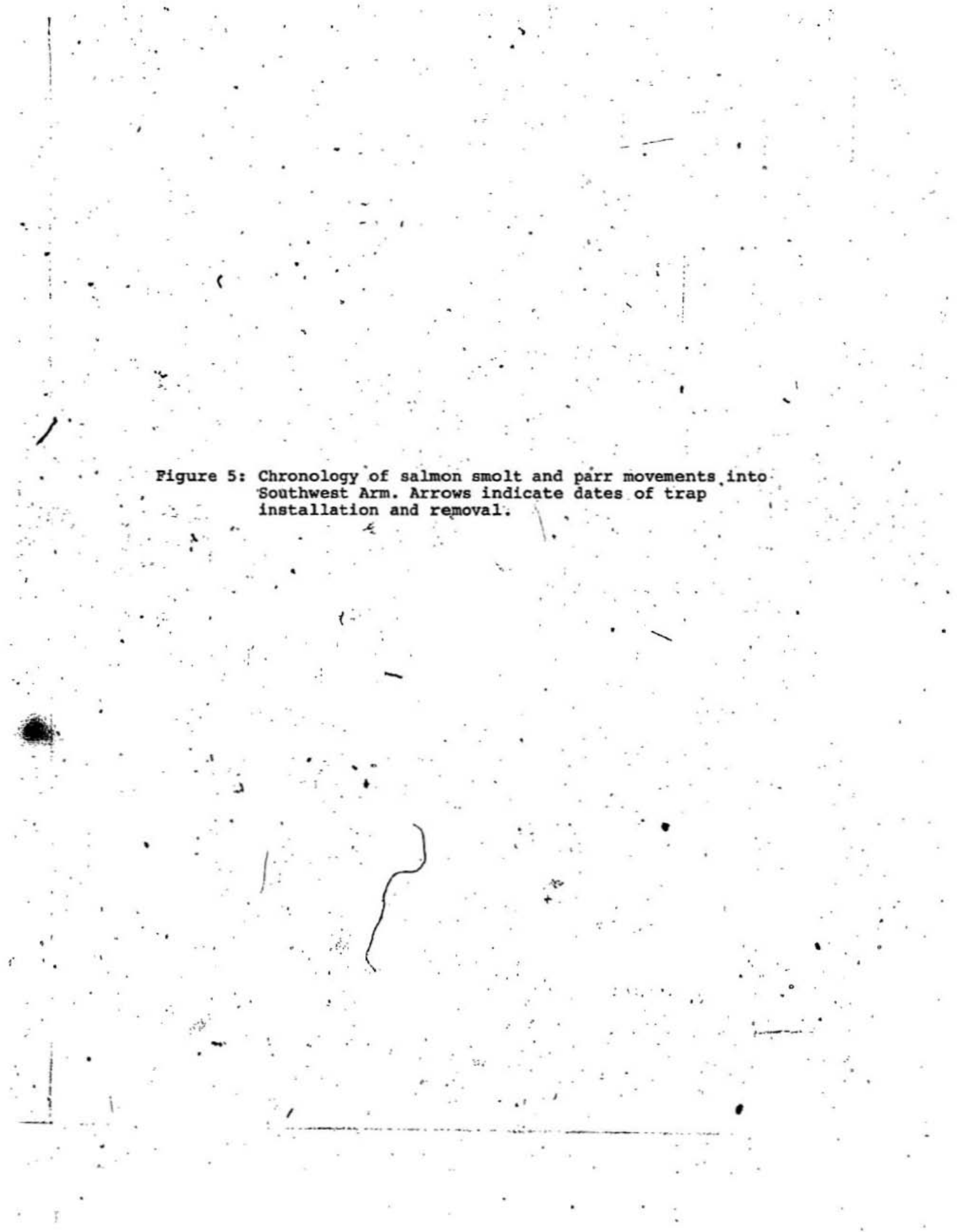


Figure 5: Chronology of salmon smolt and parr movements into Southwest Arm. Arrows indicate dates of trap installation and removal.

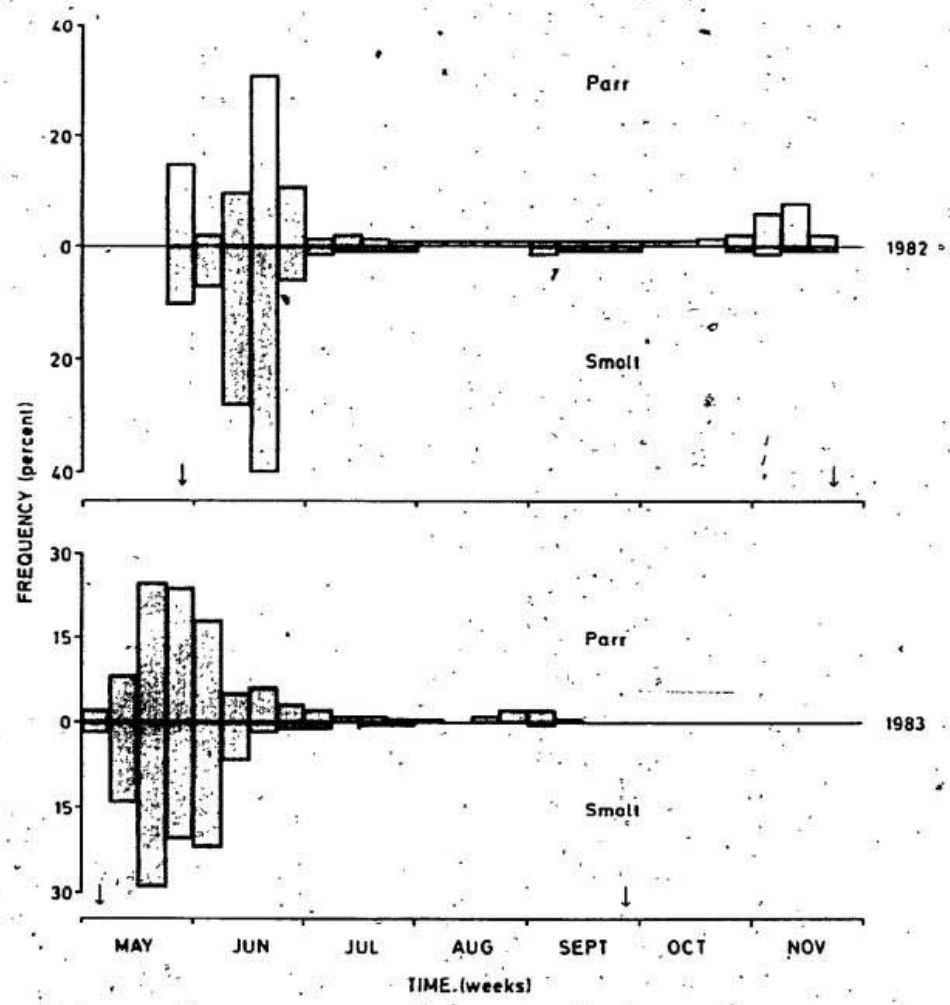

40
20
0
20
40
Parr
Smolt
1982
FREQUENCY (percent)
30
15
0
15
30
Parr
Smolt
1983
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
TIME.(weeks)

Figure 6: Length-frequency distributions of salmon parr moving into and out of Southwest Arm.

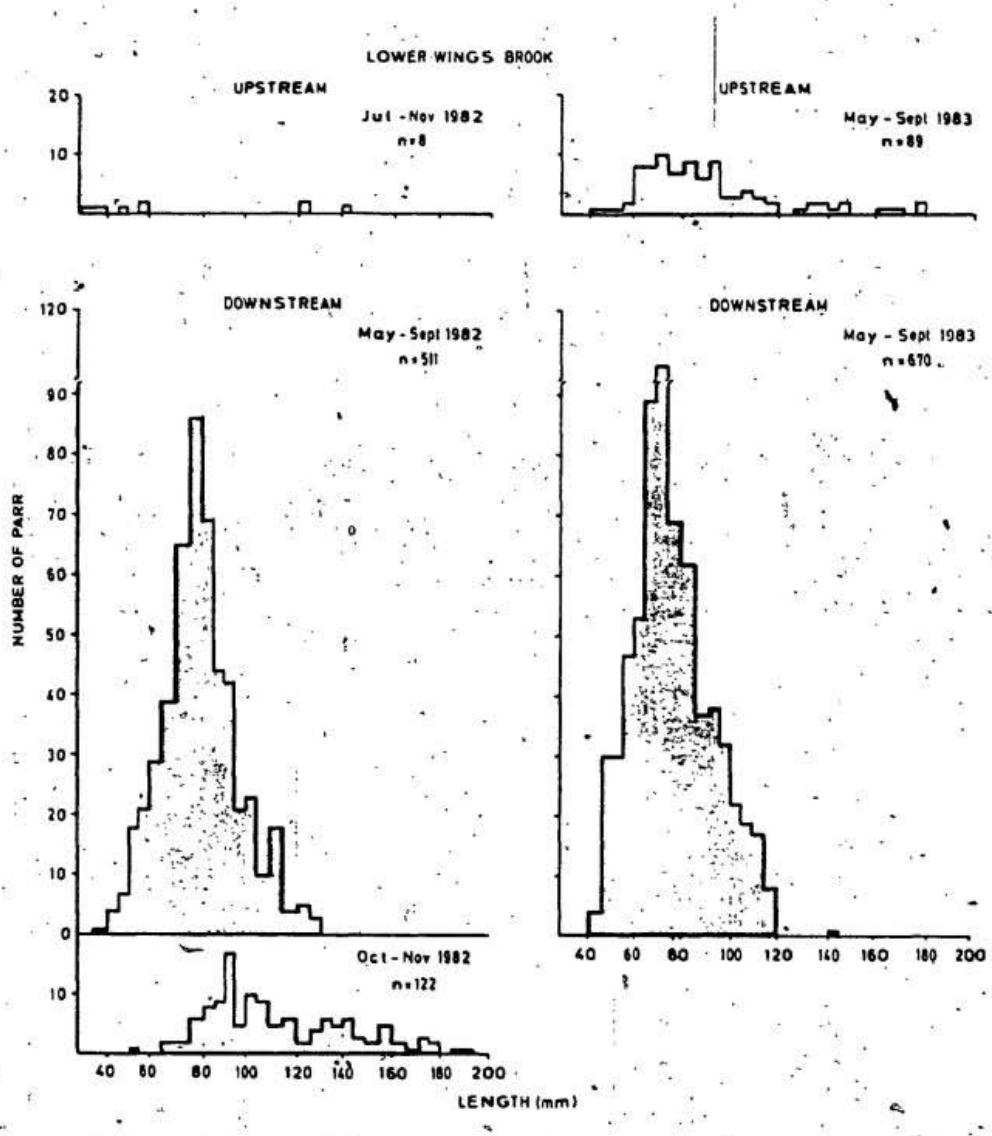

LOWER WINGS BROOK
UPSTREAM
Jul - Nov 1982
n=8
UPSTREAM
May - Sept 1983
n=89
DOWNSTREAM
May - Sept 1982
n=511
Oct - Nov 1982
n=122
DOWNSTREAM
May - Sept 1983
n=670
NUMBER OF PARR
LENGTH (mm)

Figure 7: Age-frequency distributions of salmon parr moving into Southwest Arm.

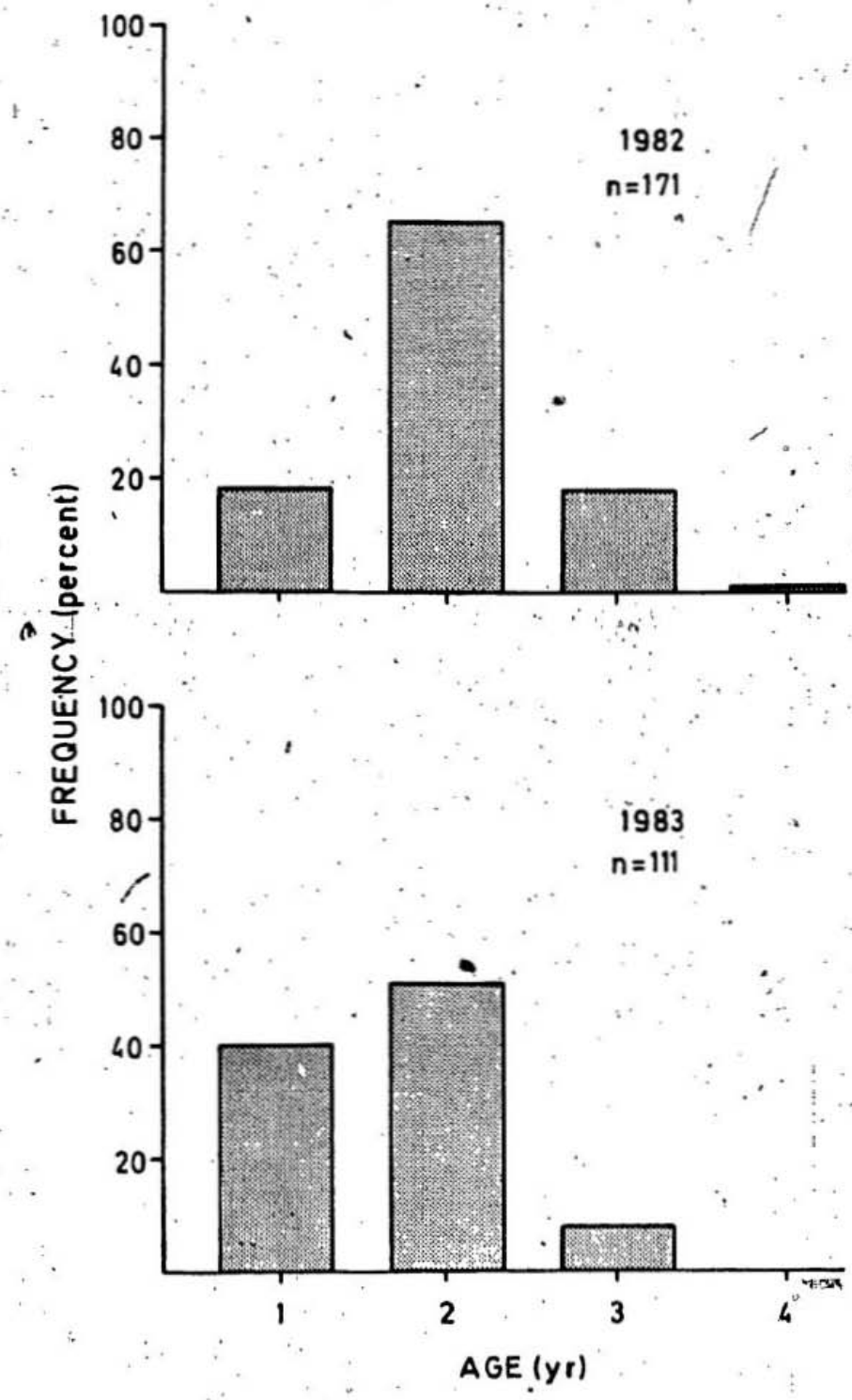

100
80
60
40
20
1982
n=171
FREQUENCY (percent)
100
80
60
40
20
1983
n=111
1
2
3
4
AGE (yr)

Figure 8: Age-frequency distributions of salmon smolt emigrating from Wings and Bluehill Ponds.

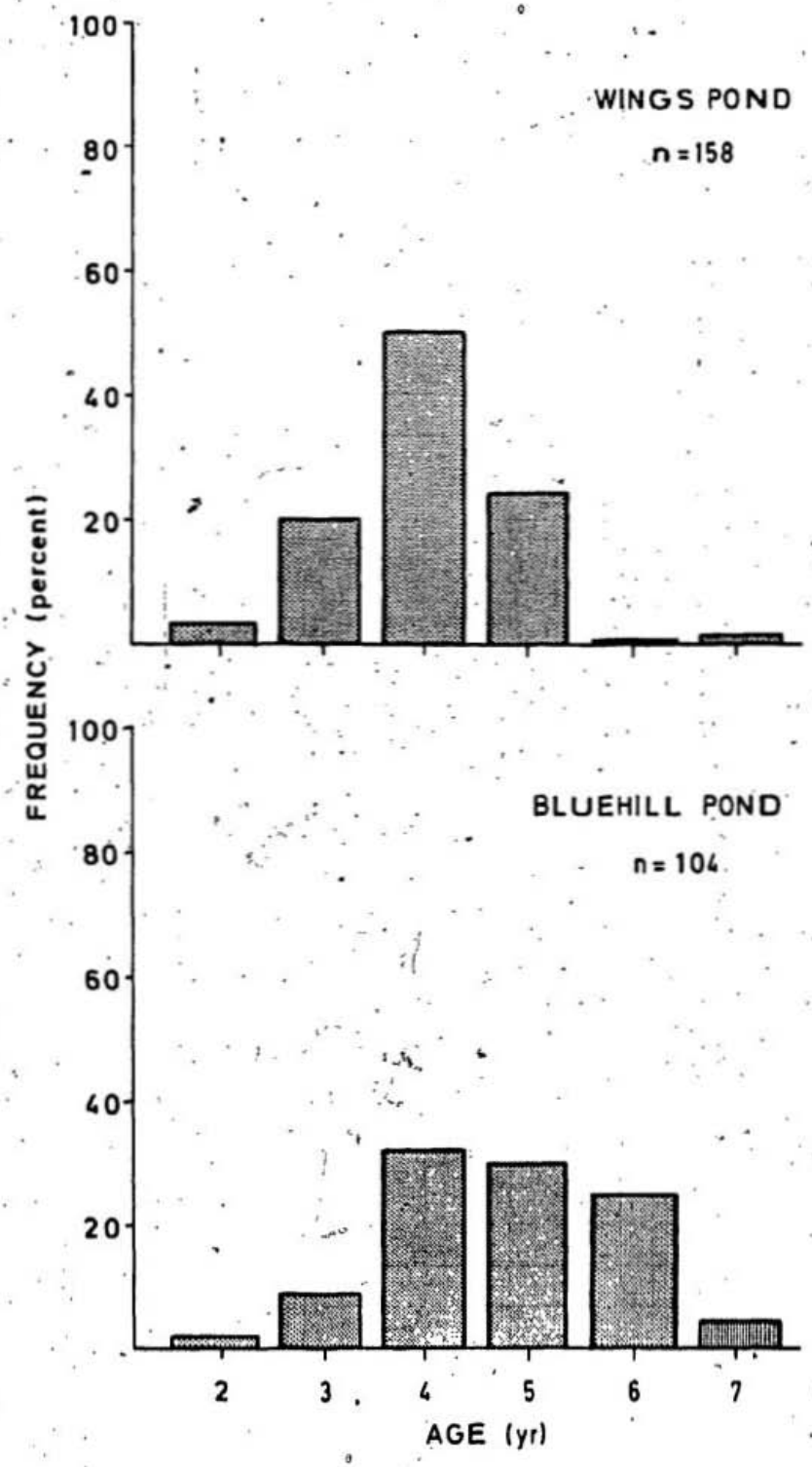
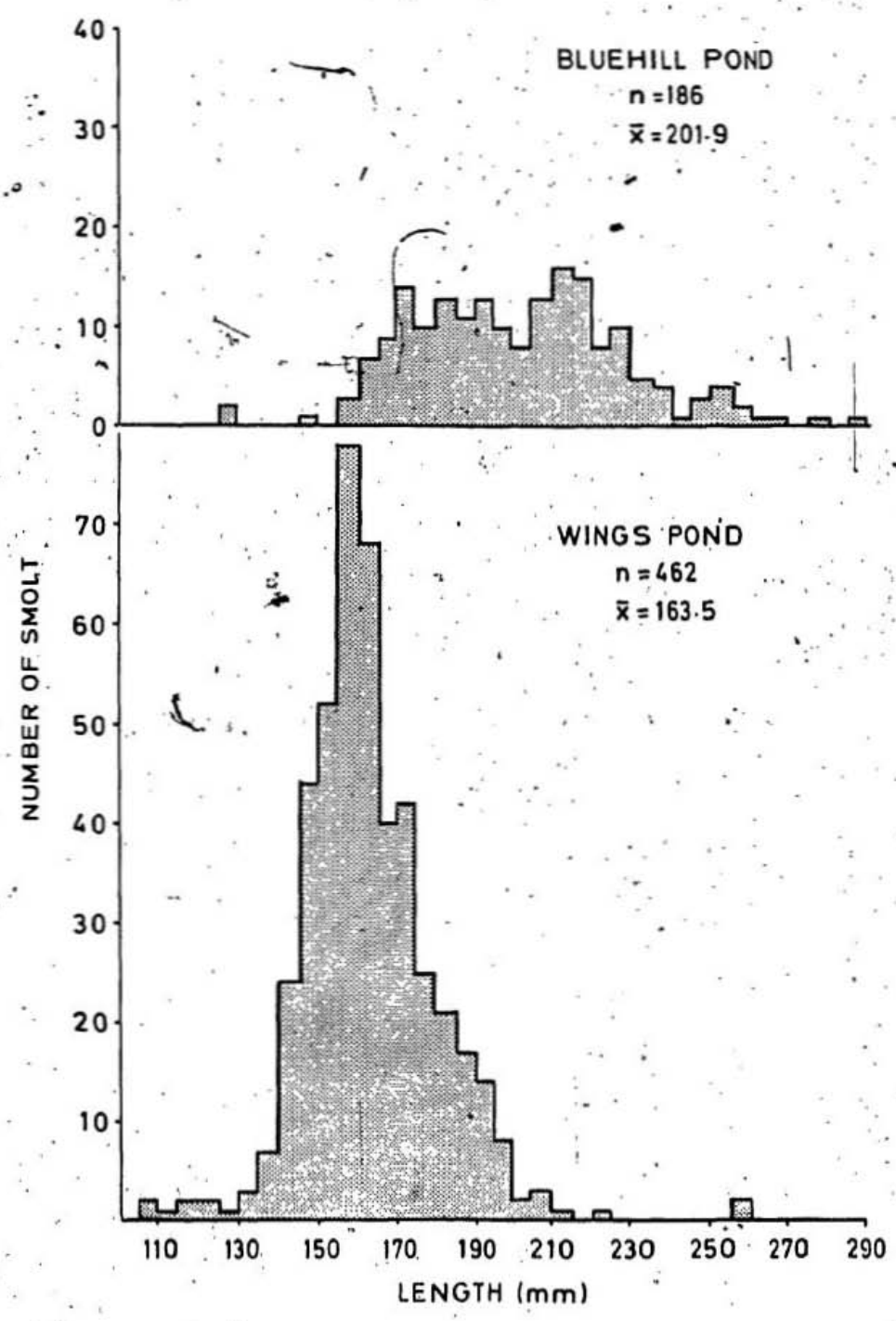

WINGS POND
n=158
BLUEHILL POND
n=104
FREQUENCY (percent)
100
80
60
40
20
2
3
4
5
6
7
AGE (yr)

Figure 9. Length-frequency distributions of salmon smolt emigrating from Wings and Bluehill Ponds.


BLUEHILL POND
n = 186
x̄ = 201·9
WINGS POND
n = 462
x̄ = 163·5
NUMBER OF SMOLT
LENGTH (mm)
0
10
20
30
40
10
20
30
40
50
60
70
110
130
150
170
190
210
230
250
270
290

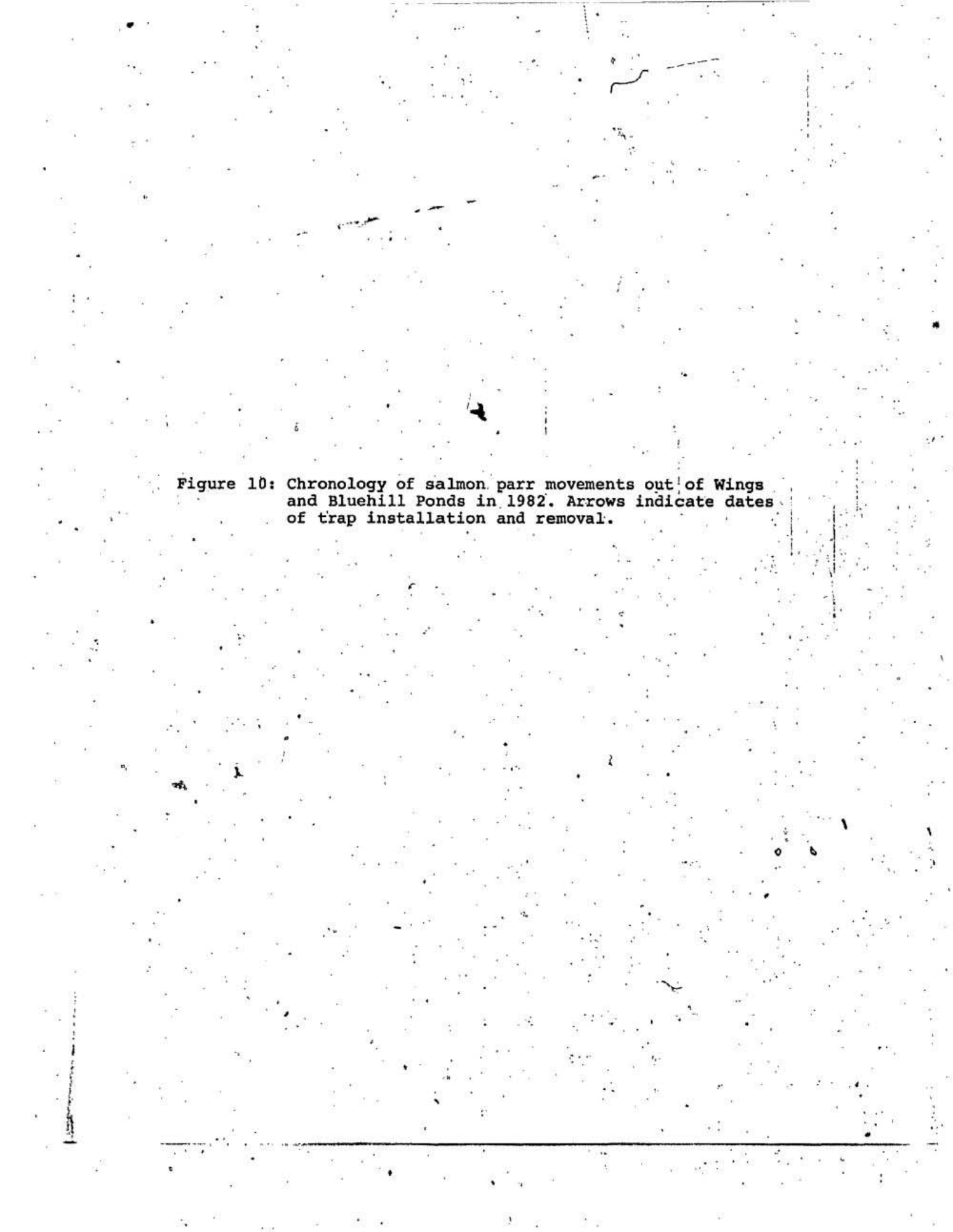


Figure 10: Chronology of salmon parr movements out of Wings and Bluehill Ponds in 1982. Arrows indicate dates of trap installation and removal.

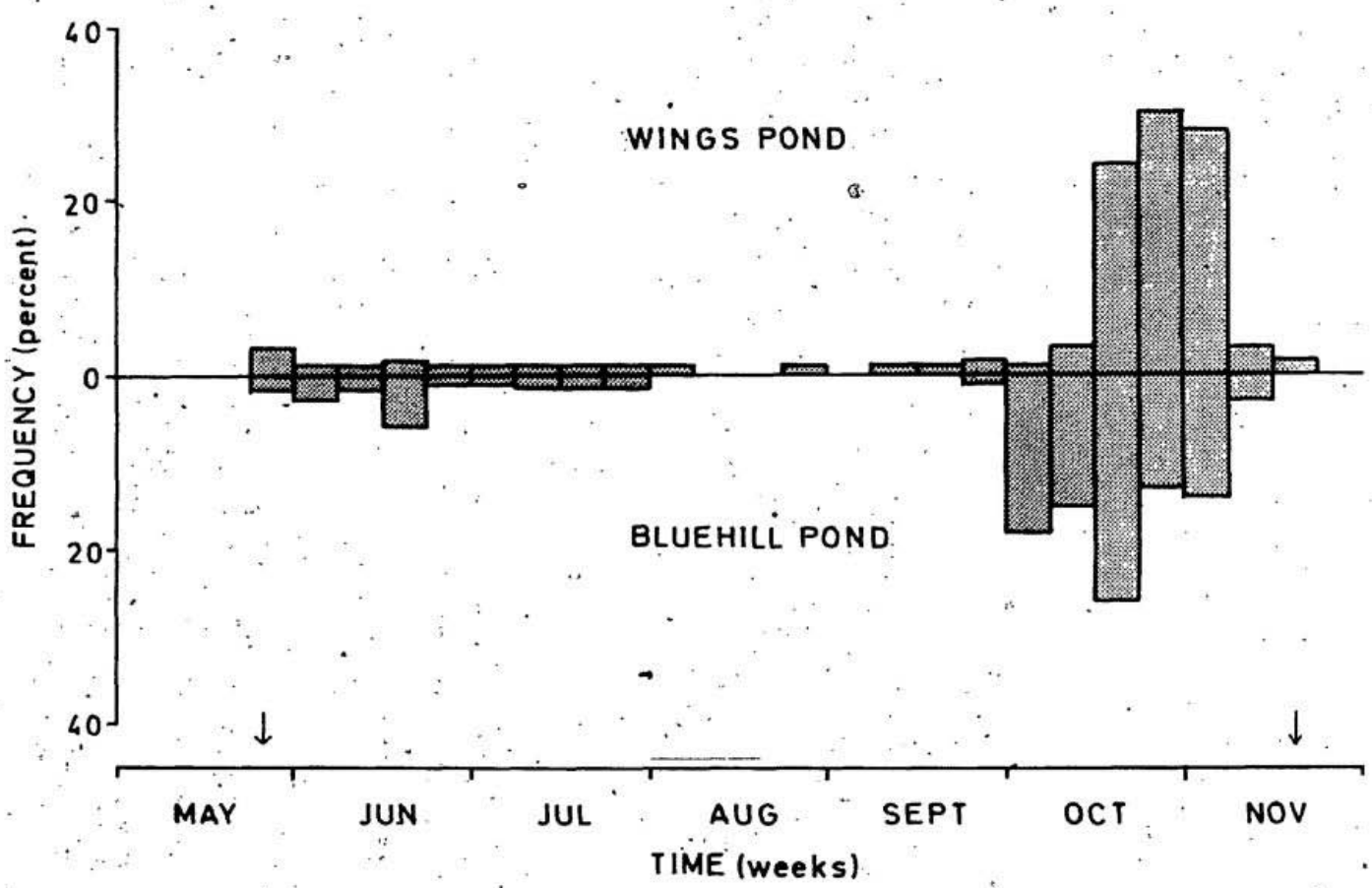

40
20
0
20
40
FREQUENCY (percent)
WINGS POND
BLUEHILL POND
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
TIME (weeks)

Figure 11: Length-frequency distributions of salmon parr moving out of Wings and Bluehill Ponds.

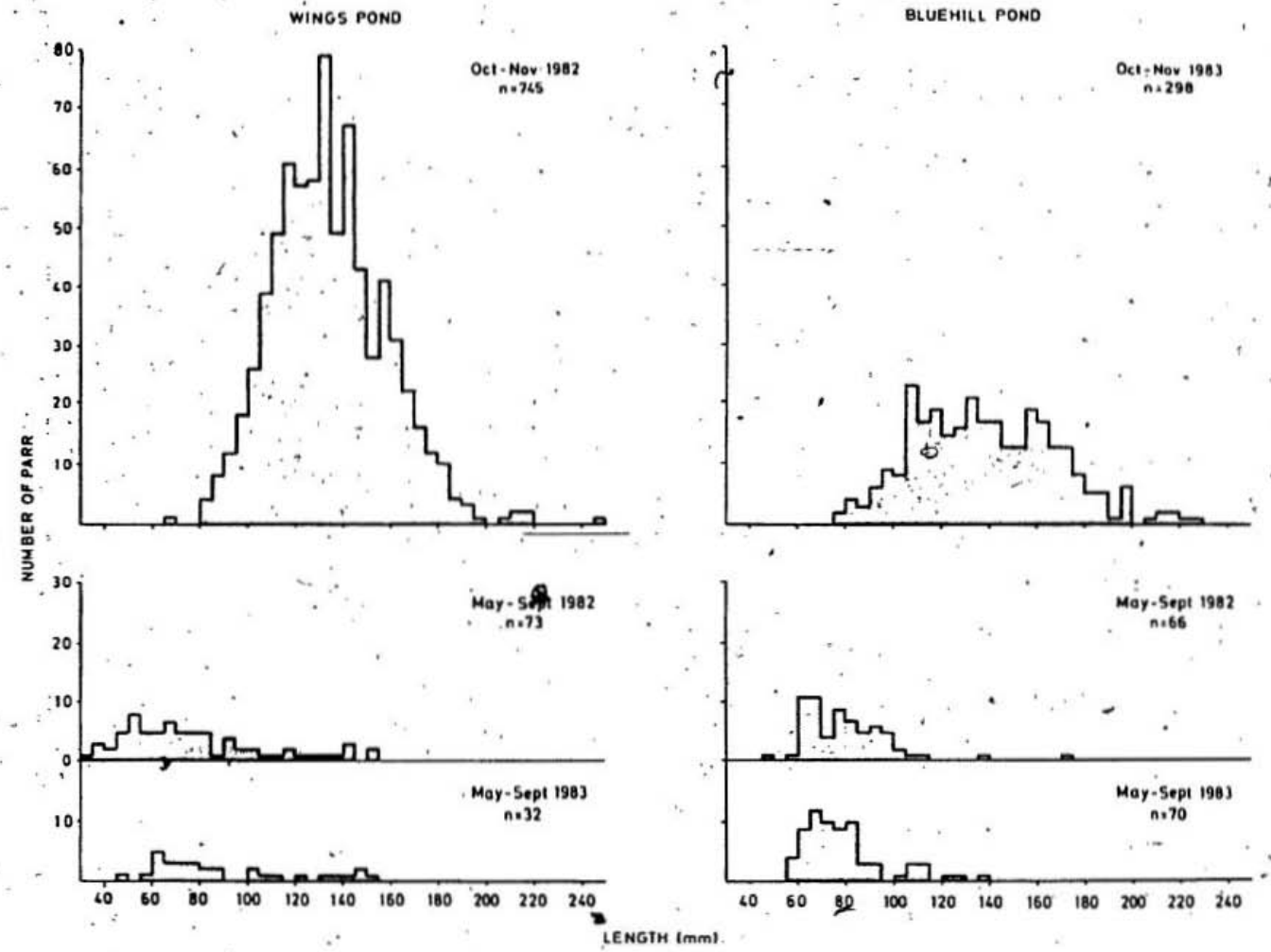

WINGS POND
BLUEHILL POND
Oct-Nov 1982
n=745
Oct-Nov 1983
n=298
May-Sept 1982
n=73
May-Sept 1982
n=66
May-Sept 1983
n=32
May-Sept 1983
n=70
NUMBER OF PARR
LENGTH (mm)
40 60 80 100 120 140 160 180 200 220 240

Figure 12: Length-frequency distributions of salmon parr collected throughout Wings Brook and its tributaries.

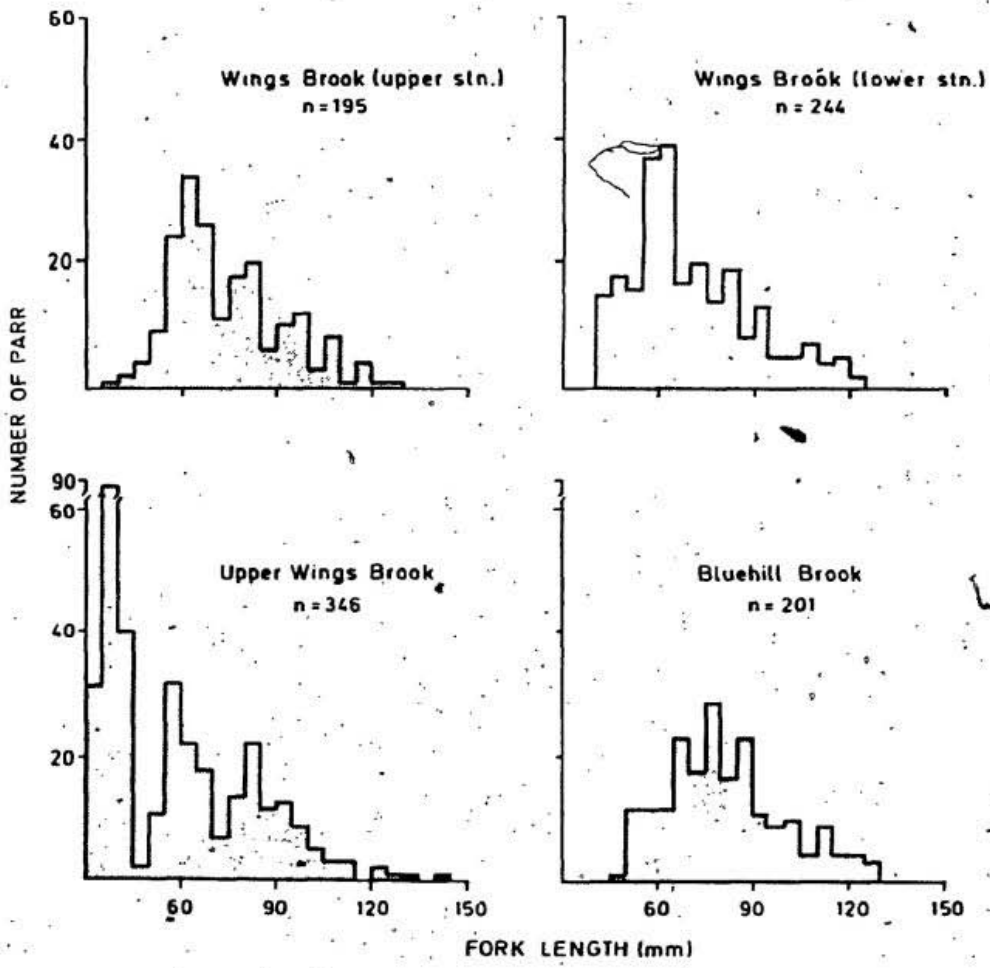
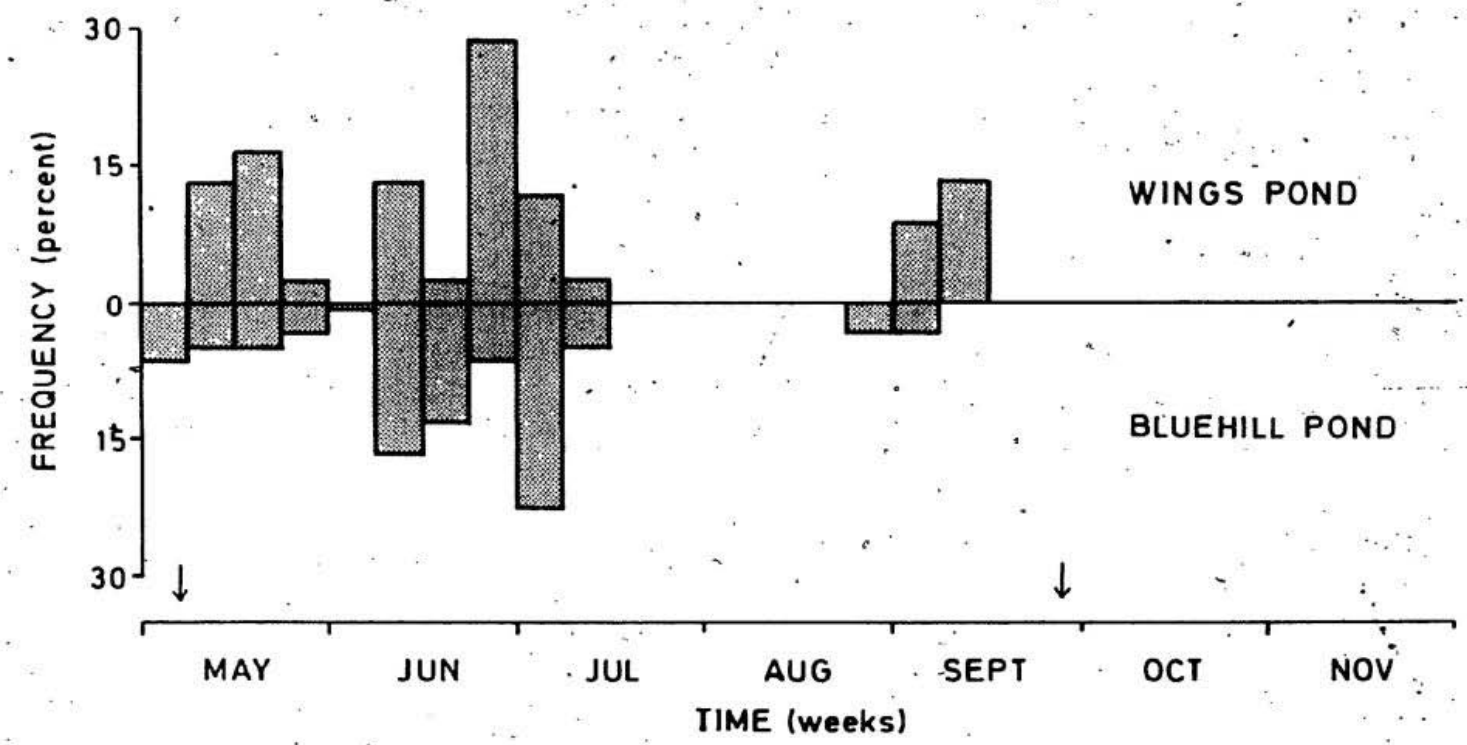

Wings Brook (upper stn.)
n=195
Wings Brook (lower stn.)
n=244
Upper Wings Brook
n=346
Bluehill Brook
n=201
NUMBER OF PARR
FORK LENGTH (mm)
60
40
20
90
60
40
20
60
90
120
150

Figure 13: Chronology of salmon parr movements out of Wings and Bluehill Ponds in 1983. Arrows indicate dates of trap installation and removal.


30
15
0
15
30
FREQUENCY (percent)
WINGS POND
BLUEHILL POND
MAY
JUN
JUL
AUG
SEPT
OCT
NOV
TIME (weeks)

Appendix A

Movements of Fishes throughout Wings Brook

Total numbers of fish moving through the counting fences of Wings Brook are presented in Table 5. The movements of Salmo salar have been outlined previously with the exception of an illustration showing the chronology of parr movements from the lakes into the streams in 1983 (Fig. 13). This figure was not included in the main text because the seasonal patterns it portrayed were misleading. Fig. 13 shows the period of greatest movement to occur in the spring when in actual fact there is relatively little movement at this time of year (Fig. 10). This misconception can be attributed to the frequency scale on the ordinate coupled with the fact that the 1983 field season did not extend into October and November, the months during which parr emigration from the lakes was at its peak.

This section will report the available data on seasonality and diel timing of movements, mean lengths, and

state of sexual maturity of brook char, American eel, rainbow smelt, threespine stickleback, Arctic char, fourspine stickleback, and ninespine stickleback in the Wings Brook system.

A.1 Brook char, Salvelinus fontinalis

The seasonality and relative magnitude of brook char movements were very similar to those described for salmon parr. Emigration from the stream occurred primarily during the spring with the numbers of fish moving either equivalent to (movement into estuary) or considerably less than (movement into lakes) the salmon. Similarly, the autumnal movement of brook char from the lakes into the stream was undertaken almost exclusively by sexually mature individuals (predominantly males).

Approximately 10-14% of the char moving into the estuary during the spring of 1983 were characterized by a silvery tinge to their scales and were presumably smolts. The mean length of 80 smolts was 15.5 + 3.0 cm (range 11.7-25.8 cm). A minimum of 22.5% of the char smolt originated in the lakes. The 1983 smolt migration commenced

with the salmon smolt migration but ended on May 30.

Char movement from the estuary into the brook was also similar to that of the parr in that more fish moved in 1983 than in 1982. An anomalous movement occurred on the morning of July 6, 1983, when 261 char ranging from 4.7-11.8 cm in length entered the upstream section of the lower Wings Brook trap. This movement was coincident with a 9.5°C increase in water temperature (17.0-26.5°C) within the previous 24 hours while water depth remained constant. A total of 15 char (9 in 1982) entering the brook from the estuary exhibited silvery colouration presumably indicative of prolonged estuarine/marine residence.

Char movements into and out of the lakes and throughout Wings Brook appear to be more random in nature than those of salmon parr (Hutchings, unpublished data). For example, many char had a propensity to move out of a lake shortly (1-5 days) after having entered it.

The diel timing of brook char movements did not differ from that of the salmon parr.

A.2 American eel, Anguilla rostrata

Only those eels moving downstream were captured in the counting fences. Eels were present in the traps during the morning checks only, indicative of nocturnal migration.

The timing of migration differed at the three sampling locations. The majority of eels emigrated from Wings Pond during the spring, whereas the main Bluehill Pond run occurred in the autumn. These seasonal differences were reflected in the timing of eel migration through the lower brook trap.

The 1982 eel emigrations from Wings Pond occurred from May 24 to June 21 (n=36), July 30 (n=1), and September 3-18 (n=11). Fifteen eels left Wings Pond from May 6 to June 21, 1983.

Eels emigrating from Bluehill Pond did so from June 1 to July 26 (n=4) and September 18 to October 5 (n=14), 1982, and on June 6 (n=1) and from August 22 to September 8 (n=21), 1983.

The spring runs at lower Wings Brook extended from May 24 until June 28, 1982 (n=43), and May 10 to June 9, 1983 (n=38). During the autumn, eels migrated from September 5 to October 20, 1982 (n=31), and August 29 to September 29, 1983

(n=51).

Mean lengths of eels moving throughout Wings Brook are presented in Table 9.

A.3 Rainbow smelt, Osmerus mordax

Collections of smelt can be separated into the seaward migration of reproductively spent adults at the mouth of Wings Brook and the incidence of yearling smelt having been transported by water currents into the traps at the lake outlets. Smelt were rarely collected in the second of two daily trap checks, suggestive of nocturnal movement.

Smelt vacated Wings Brook in exceedingly large numbers (n=4682) in 1982 and in fewer numbers (n=359) in 1983.[7] The mean lengths reported in Table 9 are based on the first 135 individuals to enter the lower trap in each year. Sex determinations were conducted in 1983 by applying pressure to the fish abdomen and identifying the gonadal substance thus extruded. The sex ratio of 149 smelt sampled

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7. Smelt generally migrate during ice break-up (Scott and Crossman 1973) so these figures are unlikely to represent the entire complement of post-spawning smelt.

throughout the run was skewed 4.1:1.0 in favour of the males. Smelt entered the estuary from May 22 to July 11, 1982, and May 4-27, 1983.

With the exception of a single 21.3 cm individual, the smelt collected in the lake outlet traps were less than 10 cm in length (Table 9), a length range appropriate for underyearling and yearling smelt (Scott and Crossman 1973). These smelt suffered mortality rates in excess of 95% as they were forced against the trap screens due to their inability to maintain position in the current. Smelt were collected in the Wings Pond trap from May 21-30, 1982 (n=128), and from May 22 to July 10, 1983 (n=6). The Bluehill Pond trap entrained smelt from October 10 to November 3, 1982 (n=19), and from May 12 until June 6, 1983 (n=165).

A.4 Threespine stickleback, Gasterosteus aculeatus

Threespine sticklebacks moved into the lower Wings Brook and Wings Pond outlet traps. There was little variability in the lengths of individuals moving at the two sites (Table 9). Movement was generally in a downstream

direction (Table 5) and was not accentuated at any particular time of the year. A gravid female measuring 7.5cm was collected in the lower Wings Brook trap on May 10, 1983.

A.5 Arctic char, Salvelinus alpinus

Juvenile Arctic char were collected at the Bluehill Pond outlet trap from November 6-8, 1982 (n=2), and from May 24 to June 6, 1983 (n=4). The char collected in 1982 were less than 10 cm in length as were those entering the stream in 1983 measuring 6.8-8.5 cm.

A.6 Fourspine stickleback, Apeltes quadracus

Four members of this species were collected in the Wings Pond outlet trap on May 21, 1982. Two individuals measured 5.1 cm and 5.3 cm in length.

A.7 Ninespine stickleback, Pungitius pungitius

Several specimens of ninespine stickleback were collected in Wings Brook Cove and in the lower reaches of Wings Brook by dip net. None were encountered at the counting fences.